Alterations in the Blood Level of Lactic Acid in Certain Salmonoid Fishes Following Muscular Activity

I. Kamloops Trout, *Salmo gairdneri*[1,2,3]

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ABSTRACT

During the summers of 1953, 1954 and 1955, experiments were carried out on the effects of muscular exercise on hatchery-raised yearling and two-year-old Kamloops trout, *Salmo gairdneri*, at the Summerland Trout Hatchery, Summerland, B.C. Following 15 minutes of vigorous exercise at 11.5°C. the blood level of lactic acid in yearlings increased from the unexercised level of 16 mg.% to 100 mg.% and then continued to increase still further during the first 2 hours of recovery to 170 mg.%, to subside in 4 to 6 hours toward the pre-exercise level. Similar changes occurred in two-year-olds, but the levels were lower in all cases, and the time course was slower. Studies were also made on hemoglobin levels, on blood glucose changes in two-year-olds, and on the relation of oxygen levels and temperature to the blood levels of lactic acid in yearlings. Cardiac rates were also measured. Observations were made on the blood level of lactic acid in moderate exercise in yearlings. The results indicate that most of the features of fatigue in the trout are in keeping with the pattern of changes in mammals. However, there were important differences in the time course of rise and fall of lactic acid to and from the blood. It is suggested that these differences may be due to the effects of lowered temperature in reducing the rate of diffusion of lactic acid between extracellular fluids and the sites of production and removal of the metabolites of muscular activity. Some implications of the results to the behaviour of fishes and death due to over-exertion are discussed.

INTRODUCTION

Much is known about man's capacity for muscular work and about the metabolic changes that make this work possible. This knowledge rests on quantitative data in terms of standard units of work, upon behaviour and the chemical changes occurring in the circulating blood during and following work in man as well as upon experimental studies on other vertebrates. The criterion for performance of work in standard units by fish has not been established as yet, and indirect methods are used, such as measuring the capacity for swimming at different rates of water flow. Observations on behaviour of fish in response to work are still meagre, as are data on changes in blood constituents following work. New information on changes in blood of fishes as well as changes in behaviour should provide some insight into the capacity of fish for moderate work, such as swimming at cruising speeds, and for severe work such as swimming at the maximum rate for brief intervals, *e.g.* the effort required in negotiating a swift passage of water upstream, or in capturing prey or escaping from predators.

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Among the many chemical changes that occur as a result of work, the conversion of muscle glycogen through several steps to lactic acid is still significant. The lactic acid so produced diffuses out to the blood stream where the level may increase tenfold in severe work, and decrease to resting levels during recovery. The restoration of muscle glycogen requires glucose which diffuses to the needy muscle from the blood stream. Many other important chemical changes occur, as may be learned from the works of Dubuisson (1954) and Mommaerts (1950).

From the work of Secondat and Diaz (1942) on lactic acid levels in the blood of the tench, *Tinca tinca*, following exercise, it would appear that the time relationships of recovery are much slower than for the human (Bang, 1936; Dill, Edwards, Newman and Margaria, 1936; Crescitelli and Taylor, 1944). Black (1955) reported for several freshwater fish that the blood level of lactic acid following activity differs greatly from species to species. Differences in the content of glycogen (Ritchie, 1926) and of lactic acid of muscle had been reported earlier for certain marine fish (Ritchie, 1927). The present investigation was undertaken in order to describe the recovery pattern from the elevated level of lactic acid in the blood of Kamloops trout, *Salmo gairdneri*, a fish that is probably more active than the tench at temperatures of 10 to 15°C. Observations were also made upon the blood glucose level during recovery. In addition, certain other studies were carried out, such as the rate of increase of the blood lactic acid level with exercise; the effect of moderate exercise; the effect of varying oxygen levels in the respired water; and a preliminary study on the effect of temperature on increased lactic acid level in the blood. The results indicate that much of the response of the Kamloops trout to muscular activity is in keeping with the changes that occur in the mammal; however, there are certain differences which would appear to be important to an understanding of the behaviour of the trout at temperatures of 10 to 12°C., differences which may be related to the lower body temperature of fish as compared with mammals.

METHODS

The experiments were carried out on hatchery-raised Kamloops trout during the summer months of 1953, 1954 and 1955 at the Trout Hatchery operated by the British Columbia Game Commission at Summerland, British Columbia.

Most of the methods have already been described (Black, 1955). The fish had been fed standard hatchery food including liver the day before the experiments were carried out. No food was given during the recovery period. Severe exercise was induced by chasing the fish continuously in a standard hatchery trough for 15 minutes. Moderate exercise was induced by exercising the trout in a rotating chamber identical to the one described by Fry and Hart (1948).

The experiments on the influence of temperature were carried out by holding yearling trout, previously exposed to 11.5°C., at 16.0°C. for 5 days in small temperature baths and then increasing the temperature to 20°C. at which temperature the trout were held for another 4 days before being exercised at 20.0°C. Control fish were held in small baths at 11.5°C.

Oxygen levels were altered by saturating water with either a stream of commercial gaseous oxygen or nitrogen. The gas was bubbled through a column filled with glass stucco beads, down which the water passed.

Most of the blood samples took longer to collect than those reported earlier (Black, 1955). The average time to collect samples from yearling trout in the following conditions after the fish was captured in the V-trough were: unexercised, 93 seconds; for fish exercised for 15 minutes an average of 109 seconds was required; for fish after 2 hours of recovery from exercise, 155 seconds. The respective times for collection of blood samples from the two-year-old trout were 68, 97 and 105 seconds. As long as 6 minutes was required for a few collections, but others were accomplished in 12 to 20 seconds.

The chemical determinations of hemoglobin and lactic acid were carried out as before except that for a very few samples, barium–zinc hydroxide filtrates were used instead of tungstic acid filtrates for the Barker–Summerson estimation of lactic acid. The Somogyi (1945) method was used for the estimation of blood glucose with one further modification since trout blood does not always hemolyze in distilled water. Hemolysis was brought about by adding the measured sample of blood to 0.66 N sulphuric acid, which after hemolysis was carefully neutralized by the addition of sodium hydroxide and the whole volume brought to 10.0 ml. by the addition of barium and zinc hydroxide as the protein precipitants. Judging by controlled experiments on fish plasma, the brief exposure to sulphuric acid of not more than 5 minutes did not alter the quantity of glucose. Moreover, the lactic acid determinations on the modified procedure for obtaining barium–zinc hydroxide filtrates, did not differ from those carried out on tungstic acid filtrates made on aliquots of whole blood.

The cardiac rate was determined by the use of a Sanborn Viso-Cardiette. Needle electrodes were inserted in the muscle of the body wall external to the pericardial cavity. A standard No. 2 lead was used. The average time to place the electrodes was 38 seconds for the yearlings and 68 seconds for the two-year-olds, while the tape was run for 24 seconds for the yearlings and 42 seconds for the two-year-olds. The fish were held inverted in the V-trough and breathed water throughout the test.

RESULTS AND DISCUSSION

Unexercised State

By unexercised state is meant the nearest approach to the resting state for fish used during daylight. As it usually took up to a minute to capture the fish and place it in the V-trough, unquestionably the fish was no longer in a rested state. The data for the unexercised state have been published before (Black, 1955) but are included here for purposes of comparison (Table I). The average value of the blood level of lactic acid in yearling trout for the years 1953 and 1954 is 15.7 ± 1.1 mg.% (milligrams of lactic acid per 100 ml. of whole blood). The standard error of the average is given after the average. The average for the two-year-old trout for the years 1954 and 1955 is 8.6 ± 0.9 mg.%. The average value for the two-year-old trout is half that for the yearlings.

TABLE I. Effect of vigorous exercise for 15 minutes on the blood levels of hemoglobin, glucose and lactic acid in yearling and two-year old Kamloops trout at 11.5°C. The standard error of the average follows the average. The range is given in parentheses below the average in certain instances. 1953, 1954 and 1955.

Age and condition	Year	No. of fish	Average weight	Average hemoglobin	Average glucose	Average lactic acid
			g.	*g. %*	*mg. %*	*mg. %*
YEARLINGS						
Unexercised	1953/54	41	57±2 (28–82)	11.0±0.2 (8.3–13.9)	—	15.7±1.1 (0–47.0)
Exercised	1953/54	35	57–3 (23–106)	10.7±0.2 (7.9–13.3)	—	99.8±1.0 (54.6–153)
TWO-YEAR-OLDS						
Unexercised	1954	11	125±18	10.1±0.4	—	8.0±0.9
Exercised	1954	11	134±12	11.2±0.3	—	82.2±10.0
Unexercised	1955	12	172±16	13.6±0.5	68±6 (40–100)	9.2±1.2
Exercised	1955	13	172±21	14.7±0.4	74±5 (40–100)	75.5±4.7
Unexercised	1954/55	23	150±13 (63–291)	11.8±0.5 (7.1–15.8)	—	8.6±0.8 (3.2–19.6)
Exercised	1954/55	24	153±13 (82–306)	13.1±0.5 (8.8–17.6)	—	78.6±6.7 (31.7–130)

It is important to know whether these values for lactic acid in the unexercised condition have been influenced by struggling efforts by the fish or by other metabolic changes that may have taken place during the period required to capture the fish, place it in the V-trough and take the blood sample. All the data for yearling trout for the years 1953 and 1954 were arranged in increasing order of the time necessary to capture and obtain blood. The values for lactic acid for the first three fish which were captured and sampled in 50 to 60 seconds were 12.5, 13.1 and 15.5 mg.%. For the last three values of the series where 210 to 240 seconds were required, the lactic acid levels were 13.8, 14.5 and 16.1 mg.%. The data for the two-year-old trout for 1954 and 1955 were also arranged in increasing time order. In the first three samples which required 40 to 42 seconds, the lactic acid values were 8.0, 6.8 and 10.5 mg.%. For the last three values in the series where 220, 225 and 360 seconds were required, the lactic acid values were 8.6, 9.0 and 14.1 mg.% respectively. Except for the last sample mentioned for the two-year-old trout, there was no consistent relationship between the lactic acid values and the total time necessary to capture the fish and take the blood samples.

The average resting basal values for the blood level of lactic acid in man expressed as mg.% are as follows: 9.9 (Edwards, 1936); 12.1 (Crescitelli and Taylor, 1944); 17.5 (Bang, 1936).

MODERATE EXERCISE

This term is used to denote a state of swimming maintained by the fish in response to a rotating chamber. The average rate of swimming accomplished by the yearling Kamloops trout at 11.5°C. in response to an arbitrary task was 10.4 ± 0.7 metres per minute (34.1 feet per minute) for the 15-minute period and 12.4 ± 0.7 metres per minute (40.7 feet per minute) for the 30-minute period.

TABLE II. Blood levels of lactic acid of yearling Kamloops trout at 11.5°C. when swimming in a rotating chamber at a sustained steady pace with an adequate oxygen supply; swimming steadily then spasmodically in a rotating chamber at a low oxygen level; and resting in chamber (stopped) with adequate oxygen.

Condition	Year	No. of fish	Average swimming rate	Average $_pO_2$	Average weight	Average hemoglobin	Average lactic acid
			metres/min.	*mm. Hg*	*g.*	*g.%*	*mg.%*
Swimming in rotating chamber for 15 min.; adequate oxygen	1953	10	9.7±0.7	129±4	63±4	11.8±0.4	28.2±5.1
	1954	10	10.6±0.7	129±2	58±4	11.0±0.3	30.3±4.2
	1953/54	20	10.2±0.7	129±2	60±3	11.4±0.2	29.2±2.2
Swimming in rotating chamber for 30 min.; adequate oxygen	1954	10	12.4±0.7	135±1	56±7	10.7±0.4	31.9±5.5
Swimming in rotating chamber for 15 min.; inadequate oxygen	1953	10	11.7±0.7	37±1	73±4	11.5±0.5	63.2±9.6
Placed in stationary chamber for 15 min.; adequate oxygen.	1954	10	—	130±2	54±3	10.9±0.4	27.5±1.7

The average lactic acid values for the two periods were 29.2 mg.% for 15 minutes and 31.9 mg.% for 30 minutes as compared with the unexercised average of 15.7 mg.% (Table II).

Bang (1936) found that, in taking blood samples during moderate exercise in man, there was always an initial rise of 8 to 30 mg.% of lactic acid in the blood, followed by a fall within 10 to 40 minutes, usually to the basal level. The fact that the lactic acid level persisted in the trout for at least 30 minutes at twice the unexercised blood level may be due to one or more of three circumstances: (a) the shift of lactic acid from the muscles due to the initial onset of work may not be completed; (b) new groups of muscles may be continually taking over the swimming effort; (c) the aerobic mechanism may not take over and keep up with even moderate activity. The work of Johnson, Edwards, Dill and Wilson (1945) showing that marked reduction in diffusion of lactic acid with lowered temperature would, together with Bang's data just cited, support the first explanation (a).

EXCITEMENT AS A FACTOR. To provide a control for the experiment on lactic acid changes in the blood stream while the fish was swimming at a moderate rate of exercise, the fish were transferred singly to the experimental chamber held in a stationary position for 15 minutes. The fish remained relatively inactive most of the time, yet the blood level of lactic acid was practically the same as that for the fish exercising in the rotating chamber (Table II).

In a similar experiment where oxygen consumption was measured, Black, Fry and Scott (1939) found that oxygen utilization was maximum when fish were transferred from the holding trough to a glass chamber in a stationary position. A prompt increase in the activity of the pectoral fins was observed in these fish. These findings point to a prompt readying response, which, as in the emergency response of mammals, must be part of the protective armament of fish.

Severe Exercise

BEHAVIOUR DURING ONSET OF FATIGUE. By severe exercise is meant the continuous chasing of the trout in a standard hatchery trough for 15 minutes.

The pattern of fatigue in the yearling Kamloops trout appeared to be uniform for each experiment. During the first minute the fish darted away from the source of stimulation at a speed of approximately 16 kilometres per hour (10 m.p.h.). Within 5 minutes and often within 3 minutes, the maximum swimming speed was reduced to approximately 3.2 kilometres per hour (2 m.p.h.). Most of the fish would stop swimming and rest on the bottom of the trough at the end of 3 minutes if permitted. During some recovery experiments, to be reported later, 3 to 5 fish were exercised at a time. In these experiments, the fish invariably swam together as a school, and as invariably stopped schooling between the 3rd and 5th minute of exercise. Moreover, the escape pattern of the fish changed within this time interval of 3 to 5 minutes, for the fish appeared to look for protection in the darker corners of the trough rather than escape by swimming. During 1953 some of the Kamloops trout appeared to be exhausted before the end of 15 minutes. This was not the case in 1954 or 1955. In a few cases the fish were allowed to rest for 3 to 5 minutes after 5 minutes of exercise. These fish were then capable of a

sustained spurt of rapid swimming for 10 to 15 seconds. No blood samples were taken from these fish.

LACTIC ACID. As a result of the severe exercise, the blood level of lactic acid increased in yearling trout from the unexercised level of 15.7 ± 1.1 mg.% to 99.9 ± 0.9 mg.% in the 15-minute period (Fig. 1). The change in two-year-old

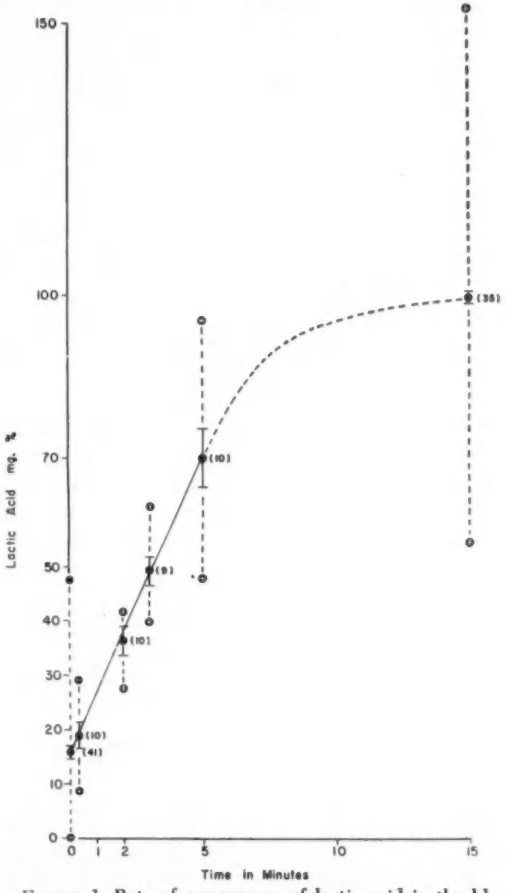

FIGURE 1. Rate of appearance of lactic acid in the blood of Kamloops trout yearlings during severe exercise at 11.5°C. 1953 and 1954.

trout following exercise was from the unexercised level of 8.6 ± 0.8 mg.% to 78.6 ± 6.7 mg.%. The spread of the data for 1954 is shown in Figure 3 and for 1955 in Figure 4.

Values for man increased from resting levels of 17.5 mg.% to 120 mg.% in 8 minutes following 1 minute of violent exercise (Bang, 1936); to an average of

128 mg.% following 16 seconds of violent exercise in four trials (Margaria and Edwards, 1934); from 13.1 mg.% to 124 mg.% for 2 minutes of exercise (Laug, 1934) and from 12.4 mg.% to 217.6 mg.% (range 117 to 328 mg.%) at the end of 5 minutes in 31 experiments of Crescitelli and Taylor (1944).

RATE OF INCREASE OF LACTIC ACID IN THE BLOOD IN RESPONSE TO VIGOROUS EXERCISE. The rate of appearance of lactic acid in the blood of trout is 10 mg.% per minute when taken between the 1st and 5th minute (Fig. 1). The rate fell off so that the rate of increase from the 5th to the 15th minute was only 3 mg.% per minute. The significance of this rate of appearance cannot be appreciated fully till the rate of production of lactic acid in the muscles is known as well as the hemodynamics. Bang (1936) has shown for man, and Flock, Ingle and Bollman (1939) in rats, that the lactic acid produced during muscular activity is produced as an initial, transitory anaerobic mechanism.

The initial rate of appearance of lactic acid in the blood of man following severe exercise ranged from 14 mg.% for the data of Bang (1936) to 100 mg.% per minute for the data of Laug (1934).

When four individual 2-year-old trout were exercised to the point of the first sign of exhaustion, the average period of exercise was 39 minutes and the range was 27 to 57 minutes. The average lactic acid value was 123 mg.%, a value which can be nearly accounted for by adding the amount that would be transferred to the blood during recovery for 24 minutes (see Fig. 3 below) to the average value of lactic acid obtained for 15 minutes of continuous exercise.

So far as the present study on trout is concerned, it would appear that the period of severe exercise used (15 minutes) is long enough to bring about maximum immediate effect of vigorous exercise at this temperature.

Influence of Oxygen Level on Lactic Acid Production

The blood level of lactic acid following 3 minutes of vigorous exercise was practically the same for the three levels of oxygen used, namely at 56, 139 and 450 mm. Hg (¼ saturation, nearly saturated and 3 times air saturation at 11.5°C.) (Table III).

TABLE III. Effect of different levels of ambient oxygen on blood lactic acid levels of yearling Kamloops trout while exercised severely for 3 minutes at 11.5° C. 1954.

Estimated time of sustained rapid swimming	Ambient P_{O_2}	No. of fish	Average weight	Average hemoglobin	Average lactic acid
	mm. Hg		*g.*	*g* %	*mg.*%
64 seconds	56	7	64±7	12.6±0.6	49.4±4.2
62 seconds	136	9	72±4	12.9±0.4	49.2±2.6
87 seconds	450	8	80±2	13.1±0.6	54.6±2.4

The effect of hypoxia and moderate exercise on the lactic acid level in the blood is shown in Table II. The hypoxic condition is below that which is necessary to maintain sustained activity in the brook trout, *Salvelinus fontinalis* (Shepard, 1955). Indeed, Shepard showed that hypoxia may stimulate activity even at relatively high levels of oxygen. The lactic acid level is significantly higher than that

observed for the steady state at near air saturation level. However, several of the fish reacted violently to the hypoxic condition, probably more actively than the brown trout fry, *Salmo trutta* described by Jones (1952).

Edwards (1936) found in man performing work at high altitude that before acclimatization to the reduced pressure of oxygen occurred, there was a higher output of blood lactic acid for the same amount of work output at sea level. Jervell (1928) found that the blood lactic acid increased in man when the oxygen content of the inspired gas fell below 7.5%. In more recent work, Asmussen, Dobeln and Nielsen (1948) have found in man that at decreased oxygen levels, the capacity for work was lowered but the maximum level of blood lactic acid was practically the same or higher than when the same amount of work was performed while breathing air. They also found that while breathing pure oxygen, the capacity for work was increased, but that the maximum level of lactic acid in the blood was the same as when air was breathed. These latter findings appear to obtain for the Kamloops trout as well (Table III).

The foregoing studies on the Kamloops trout are considered as exploratory. From the work of Shepard (1955) it is clear that the maximum rate of sustained moderate work must be exacted from the fish in order to elucidate the relation of oxygen levels to performance. These conditions were not controlled in the present study.

Effect of Temperature

During 1955, yearling Kamloops trout were acclimated to 20.0°C. No difference was found in the blood level of lactic acid from the controls carried out at the temperature of 11.5°C. (Table IV). Graham and Gibson (1948) found that

Table IV. Effect of temperature upon the blood levels of lactic acid in yearling Kamloops trout following 15 minutes of vigorous exercise at two temperatures of acclimation. 1955.

Temperature of acclimation	Number of fish	Weight	Hemoglobin	Lactic acid
°C.		*g.*	*g.%*	*mg.%*
11.5	9	54±5	13.4±0.6	100±7
20.0	12	47±2	13.5±0.7	105±7

the consumption of oxygen during moderate activity continued to increase up to 20.0°C. They also found that the cruising speed was greater at 25.0°C. than at the lower temperatures beginning at 10.0°C., although the rate of increase in cruising speed began to diminish at about 15.0°C.

The influence of temperature upon the blood levels of lactic acid following activity, both moderate and severe, should be extended to include recovery from fatigue products. Moreover, a wider range of temperatures should be investigated.

Blood Glucose Levels

There was no immediate significant change in blood glucose following 15 minutes of vigorous exercise (Table I). Secondat (1950) observed a slight but

not a significant increase in the blood glucose of carp, *Cyprinus carpio*, following vigorous exercise at 6 to 8°C. and 18 to 22° C. Simpson (1926) found no significant change in blood glucose immediately following activity in the brown bullhead, *Ameiurus nebulosus*, nor did Kiermeir (1939) in the comprehensive study she made of brown trout. In man, blood glucose may rise immediately in vigorous exercise where an emotional factor is present (Best and Partridge, 1930), or show a slight decrease in severe treadmill experiments (Edwards, Richards and Dill, 1931), or rise in the first 30 minutes then decrease in the next 30 minutes in experiments performed on a bicycle ergometer (Boje, 1936).

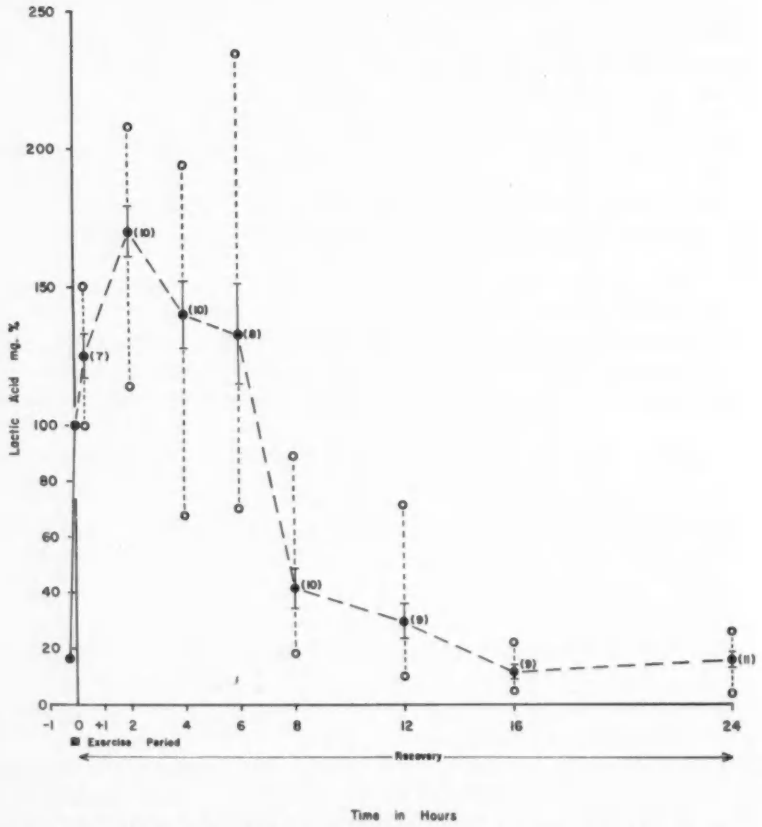

FIGURE 2. Alterations in the blood level of lactic acid in yearling Kamloops trout following 15 minutes of severe exercise at 11.5° C. The recovery changes are shown by the broken line. The number of data is shown beside the average which is represented by a solid circle. The range is shown in open circles and the distance between the vertical bars represents twice the standard error of the average. 1953 and 1954.

Recovery Period Following Vigorous Exercise

lactic acid. The changes that occur in the blood level of lactic acid in yearling Kamloops trout following vigorous activity for 15 minutes are illustrated in Figure 2. The average lactic acid increased to near 100 mg.% during the exercise and then increased to 170 mg.% at the end of 2 hours of recovery, and did not subside below the level of 100 mg.% for 6 hours. By the end of the 8th hour the

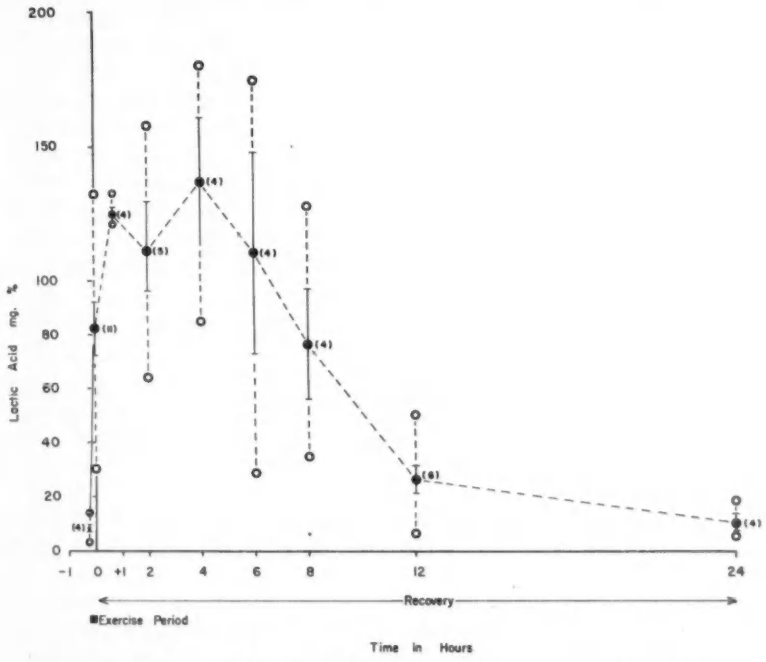

Figure 3. Alterations in the blood level of lactic acid in two-year-old Kamloops trout following severe exercise for 15 minutes at 11.5° C. 1954.

level had diminished to around 40 mg.%, but a return to the pre-exercise level did not occur till the 16th hour of recovery.

A similar pattern was observed for the 2-year-old Kamloops trout, both for 1954 (Fig. 3) and 1955 (Fig. 4). In the 1954 data (Fig. 3), the drop in lactic acid was about 2 hours slower than the recovery for the yearlings (Fig. 2). However, there is a considerable variation in the data as shown by the standard errors of the averages. In the 1955 data there is a considerable drop at the end of the 4th hour; however, the average is not significantly different from that obtained for the 6th hour of recovery. From evidence published elsewhere (Black, 1956) it would appear that a half load of lactic acid diminishes to the unexercised level in about 40 minutes in 2-year-old Kamloops trout.

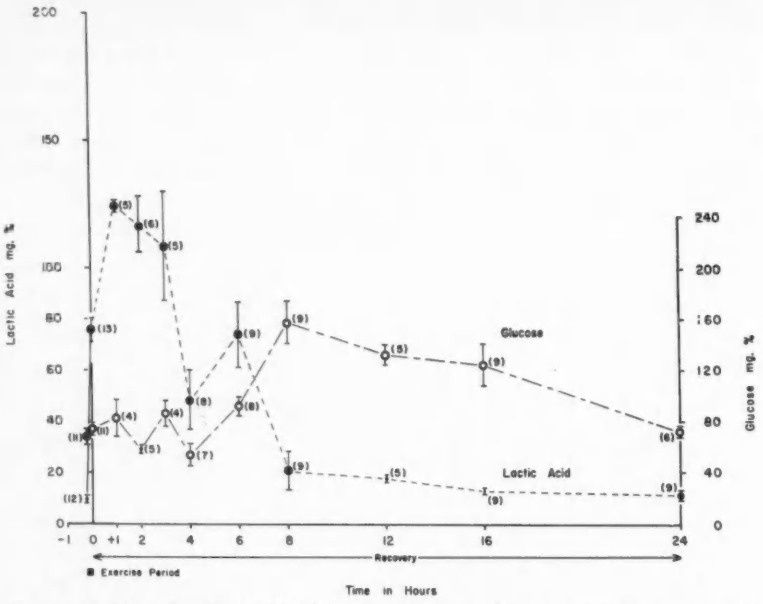

FIGURE 4. Alterations in the blood levels of lactic acid and glucose in two-year-old Kamloops trout following severe exercise at 11.5° C. The averages for the lactic acid are shown as solid circles and for the glucose as open circles. For the sake of clarity the ranges were omitted. 1955.

A tendency toward an increase in the blood level of lactic acid after 6 hours of recovery is seen in four out of the ten cases for the tench reported by Secondat and Diaz (1942).

In man the decline in the blood level of lactic acid begins as soon as the severe exercise is ended, or may increase for 10 minutes and then subside (Bang, 1936; Crescitelli and Taylor, 1944). The return of lactic acid to approximately the resting level was complete in 50 to 60 minutes in these experiments on man.

There are at least three possible reasons why the lactic acid may continue to increase and take so long to subside in the trout at this temperature of 11.5°C. The most likely reason, which is based on the work of Johnson, Edwards, Dill and Wilson (1945), on diffusion of lactic acid across the mammalian red cell is that the lactic acid diffuses slowly from the muscles and thus continues to flood the circulating body fluid for a long time. They found that the time necessary for one half of the product to diffuse across the human red cell membranes was 2 minutes at 36°C.; 25 minutes at 14°C.; and 20 hours at 0°C. A second possible reason is that the liver and other organs and tissues which may utilize or excrete lactic acid, may fail to function rapidly, again because of the lowered diffusion rate. A third possibility is that the rate of circulation may be seriously reduced by the effect of acid upon the heart, for Redfield and Medearis (1926) showed that the ability of turtle heart muscle to perform work decreased in proportion to the

increase in lactic acid. Evidence relating to the latter possibility is presented below.

Whatever the basis may be for the prolonged presence of lactic acid in the blood of trout following the relatively short burst of sustained vigorous activity, there can be no question that the delay in removal must be limiting to the swimming activity of the trout. As recounted before (Black, 1955) the Kamloops trout may recover quickly to make another rapid spurt, but this second rapid swimming effort was of very short duration, 10 to 15 seconds in all. The reduction in maximum swimming rate from 16 kilometres per hour (10 m.p.h.) to 3.2 kilometres per hour (2 m.p.h.) must surely be of importance in survival with respect to migration against swiftly moving or cascading waters.

The long period for the removal of lactic acid from the blood must reduce the loading of oxygen at the gills in fish blood that possesses a large Bohr effect as is likely the case for Kamloops trout (Black, 1955). There is the possibility, of course, that lactic acid may be excreted by the gill as well as the kidneys, or that the displacement of carbonate or other anion is sufficient to buffer adequately. In this connection, von Buddenbrock (1938) found that blood passing through the gills of cod suffering from exertion was still dark in colour. Secondat (1950) reported that the oxygen capacity of carp was reduced following severe muscular exercise. Auvergnat and Secondat (1942) found that two hours after severe exercise in the carp, the pH (7.24) was still down and did not approach the resting level (pH = 7.33) till the sixth hour of recovery (pH = 7.31). In these experiments the blood level of carbon dioxide fell immediately from 35 to 17.5 volumes % with activity at which latter time the pH was 7.25.

The slow removal of lactic acid from the trout at 11.5°C. should be considered in an analysis of oxygen debt in fishes. Bang (1936) showed in man that the lactic acid removal from the blood occurred long before the oxygen debt was repaid. Keys (1930), Spoor (1946), Fry (1947) and his students (Job, 1955; Shepard, 1955) have anticipated the difficulties of an oxygen debt history by subjecting the fish to a long period of rest before determining the minimal level of oxygen utilization.

The possibility that lactic acid and other correlates of vigorous activity are the basis of death following exertion has already been raised by von Buddenbrock (1938) and Huntsman (1938) for marine fishes. Further support for this view is given by Smith (1955) who states that large fishes taken alive after a struggle on a line rarely survive and that even harpooned fish show a greater survival-rate than those taken on a hook. In a recent paper (Black, 1956) the suggestion is made that lactic acid and related *sequelae* from vigorous muscular activity are the cause of delayed planting mortality which occur in trout (Horton, 1956).

GLUCOSE. Changes in blood glucose during recovery from exercise are shown for two-year-old Kamloops trout in Figure 4. The glucose did not change significantly immediately following exercise. There is a significant rise in glucose between the 6th and 8th hour of recovery, during which interval there is a significant fall in the blood level of lactic acid. The blood glucose returns to the pre-exercise level by the end of 24 hours of recovery. Boje (1936) found in man

that the blood glucose rose during exercise (25 to 60 minutes duration) then continued to rise slightly when the exercise stopped and subsequently declined in seven of eight trials.

Himwich, Koskoff and Nahum (1928) showed, in dogs, that blood lost a greater amount of lactic acid as it passed through the liver than it did on passing through any other organ, and that simultaneously glucose was added to the blood from the liver. Long and Grant (1930) showed that in rats the body glycogen was restored in 12 hours after activity, whereas the lactic acid from the blood and the body was removed in 1 to 2 hours; that the glycogen content of the liver was not greatly altered by exercise during recovery, and that the blood sugar fell during exercise, but was restored rapidly to normal. It will be interesting to determine whether similar changes occur in fishes.

CARDIAC RATES. Cardiac rates, as measured by the electrocardiograph, are shown in Table V. From these data it is evident that, under the conditions in

TABLE V. Cardiac rates in yearling and 2-year-old Kamloops trout following exercise at 11.5° C. 1955.

Age	Condition	Number of fish	Weight	Average respiratory rate	Average cardiac rate
			g.	*per minute*	*per minute*
Yearling	Unexercised	11	58±3 (44–84)	115±6 (86–148)	54±5 (25–72)
"	Exercised 15 minutes	6	49±7 (31–82)	125±6 (117–142)	61±2 (56–67)
"	Recovered 2 hours after exercise	6	48±4 (31–62)	124±3 (115–133)	55±4 (40–69)
2-year-old	Unexercised	10	123[a] (90–160)	110±5 (88–140)	55±5 (28–72)
"	Exercised 15 minutes	6	218[b] (180–257)	122±3 (116–124)	60±5[c] (23–115)
"	Recovered 2 hours after exercise	6	167±25 (122–244)	125±4 (110–134)	54±7 (24–79)

[a]4 readings.
[b]2 readings.
[c]No heart beat in 2 out of 8. These data were not included in the average.

which the readings were taken, there is no significant change in cardiac rate with exercise or during recovery, except for the two instances where the heart beat could not be detected after exercise. These experiments were carried out for the reason that repeatedly the time taken to obtain blood samples indicated that the cardiac output must have been reduced by severe exercise, both immediately and during the recovery period, or that the cardiac puncture was more injurious to exercised fish. However, if indeed there is a reduction in cardiac output, the change probably cannot be attributed always to a reduction in cardiac rate.

In man, the pulse rate doubles with severe work (Bowen, 1904). From the data given in Table V it would appear that the cardiac rate does not change greatly with exercise. However, this conclusion may not be warranted for the cardiac rate was not measured in a truly resting condition, for the fish had been disturbed sufficiently for the lactic acid to have increased within the 2 minutes taken for the experimental procedure (Table V).

SUMMARY

1. The average blood level of lactic acid in the unexercised condition in yearling Kamloops trout was 15.7 ± 1.1 mg.%, and in two-year-olds the level of lactic acid was 8.6 ± 0.8 mg.%, while the blood glucose was 68 ± 6 mg.%.

2. During moderate exercise represented by a cruising speed of 10.2 metres per minute (33.5 feet per minute) the blood level of lactic acid in yearling trout was 29.2 ± 2.2 mg.%, and approximately this level persisted through 30 minutes of such exercise.

3. Excitement of transfer from a holding trough to the experimental chamber increased the blood level of lactic acid to 27.5 ± 1.7 mg.% in yearling trout which did not appear to be active.

4. As a result of severe and continuous exercise in water at 11.5°C. for 15 minutes, during which time the swimming rate decreased, the blood levels of lactic acid increased to 99.9 ± 1.0 in yearling trout and to 78.6 ± 6.7 mg.% in two-year-old trout.

5. The concentration of lactic acid in the blood of yearling trout increased at the rate of 10 mg.% per minute during the first 5 minutes of severe exercise, and at the rate of 3 mg.% per minute during the last 10 minutes of the 15-minute period.

6. The half load of lactic acid in the blood of yearling trout was attained at the end of 3 minutes of severe exercise. This time was not altered when the ambient oxygen pressure was reduced to a third of air saturation (56 mm. Hg), or increased three times air saturation at 11.5°C. (450 mm. Hg).

7. Raising the acclimation temperature to 20.0°C. from 11.5°C. did not alter the blood level of lactic acid in yearling trout resulting from 15 minutes of severe exercise.

8. During recovery from the 15 minutes of severe exercise the blood level of lactic acid of yearling trout increased to 170 mg.% in 2 hours, and did not subside below 100 mg.% for 6 hours. By the end of the 8th hour the level had decreased to 40 mg.%, but the pre-exercise level was not attained till 16 hours of recovery had occurred.

9. The pattern of changes in the blood levels of lactic acid was similar in the two-year-old trout, but the recovery was slower and the levels attained were lower than for the yearling trout.

10. The blood level of glucose in two-year-old trout did not alter immediately with severe exercise, but the level increased significantly between the 6th and 8th hour of recovery (to 157 ± 16 mg.% at the 8th hour), during which interval the lactic acid declined.

11. Except in two cases out of eight where no electrical activity of the heart was recorded, there was no significant change in the average cardiac rate with activity or recovery under the special conditions of the experiment.

12. In most details, the response of the blood lactic acid levels to muscular activity appears to be the same in fishes and mammals. However, there are some differences, especially in the delayed increase of lactic acid in the blood of fishes after severe exercise, and the longer period of decline. These differences are

ascribed to the slower rate of diffusion of lactic acid at the lower temperature in fishes. These differences in appearance and removal of lactic acid may be the basis for the death of fishes due to exertion. The marked decline in the maximum swimming rate following a short sustained spurt of activity may also be of significance in the survival from predators or in the capture of prey, and to the migration up swiftly moving waters. The incidence of the end-products of fatigue also should be considered in all experiments dealing with the study of physiological properties of the blood especially oxygen and carbon dioxide dissociation curves. A history of fatigue probably will influence studies on gaseous metabolism in fishes, even more than has been demonstrated in mammals.

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Salmon Tagging at Francis Harbour Bight, Labrador[1]

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ABSTRACT

Francis Harbour Bight, situated near the southern end of the Labrador coast, was the centre of tagging operations in 1950. During the period June 28 to July 18, 74 salmon and 41 grilse caught in commercial gear were tagged. In this area the salmon run extends from June 10 to July 31 with the peak around June 30, and the time of the grilse run is from July 1 to August 15 with the peak around July 20. Thus the tagging period covered the last half of the salmon run and the first part of the grilse run.

There was a 15% return of tagged salmon which is considered to be fairly representative. All the recaptured salmon were taken in Labrador by commercial gear. The distribution north and south of the tagging area was equal and extended to the northernmost limit of the commercial salmon fishery. The greatest distance travelled by a recaptured salmon was 186 miles, and the fastest rate of travel was 17 miles per day.

The small return of tagged grilse of just over 7% is indicative of low fishing effort. The fishermen here are mainly concerned with procuring the larger salmon and in prosecuting the cod fishery.

INTRODUCTION

Francis Harbour Bight is a small fishing settlement on the Labrador coast about 65 miles north of the northern end of Newfoundland. The settlement is on an island in Alexis Bay, and the fishermen live there during the summer to prosecute the cod fishery mainly. They move inland for the winter where firewood is plentiful and hunting is pursued.

The duration of the salmon (*Salmo salar*) fishery in this area is about 2 months. The salmon (2-sea-year and older fish) run extends approximately from June 10 to July 31 with the peak occurring around June 30. The time of the grilse (1-sea-year fish) run is 2 to 3 weeks later, namely July 1 to August 15 with the peak around July 20.

Gill nets only are used in this fishery, the majority of the nets being 6-inch mesh. The catch of grilse is consequently small because it is possible for most grilse to pass through a 6-inch mesh. No salmon traps are used. They have been tried without success. The reason the fishermen give for their failure is that the salmon will not lead along the net into the trap because of the strong current. A similar situation exists in the Cape Charles and Battle Harbour areas which are south of Francis Harbour Bight. Very few salmon or grilse are caught in cod traps in the Francis Harbour Bight area although they are fished during the second half of the salmon run and throughout the grilse run. This may be due to several things in addition to the reason already given for the failure of salmon traps: they are not set in good salmon berths; the majority of them are set 10

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to 12 feet beneath the surface; and the average mesh size of the leader is 7 inches. Farther north, however, previous to the Second World War when the cod fishery was prosecuted very extensively on the Labrador coast, large numbers of salmon and grilse were often taken in cod traps.

The majority of the nets in the Francis Harbour Bight area are set around several small islands. Judging by the way the salmon are meshed in the nets they do not appear to run in any one direction. Best catches are made when the winds are northeast to east which are onshore winds. Also, fishermen here claim catches are affected by ice conditions. They think that salmon coming to the coast trim along the edge of the ice and that very good catches are obtained near each end of the ice and poor catches on the part of the coast covered late with ice.

In 1950, 74 salmon, 41 grilse, and 3 kelts were tagged during the period June 28 to July 18 (Table I). The tagging period covered the last half of the

TABLE I. Number of salmon and grilse tagged daily and the approximate time of the runs as indicated by the fishermen.

Date, 1950	Number tagged	
	Salmon	Grilse
June 10	(first of run)	
" 28	1	
" 29	3	1
" 30	4 (peak of run)	2
July 1	4	1 (first of run)
" 2	17	1
" 3	17	4
" 4	...	1
" 5	3	3
" 6	3	...
" 7	3	...
" 8	3	5
" 9	1	2
" 10	2	...
" 11	1	2
" 12	3	...
" 13	1	4
" 14	...	1
" 15	1	1
" 16	5	2
" 17	1	7
" 18	1	4
" 20	...	(peak of run)
" 31	(end of run)	...
Aug. 15	...	(end of run)
Total	74	41

salmon run and the first part of the grilse run. The fish were caught in gill nets by commercial fishermen within a radius of 1 mile of the settlement of Francis Harbour Bight. The tagging was done in the fishermen's boats by two taggers who worked independently. The type of tag and tagging methods were the same

as those used in tagging operations at Bonavista in 1940 (Blair, 1956). A reward of $1 was offered for return of a tag. No additional effort was made to recover tags.

TAGGED SALMON
(excluding grilse)

The salmon fishery in 1950 was considered fair by the fishermen. The number of salmon tagged (Table I), however, was small because the peak (June 27 in

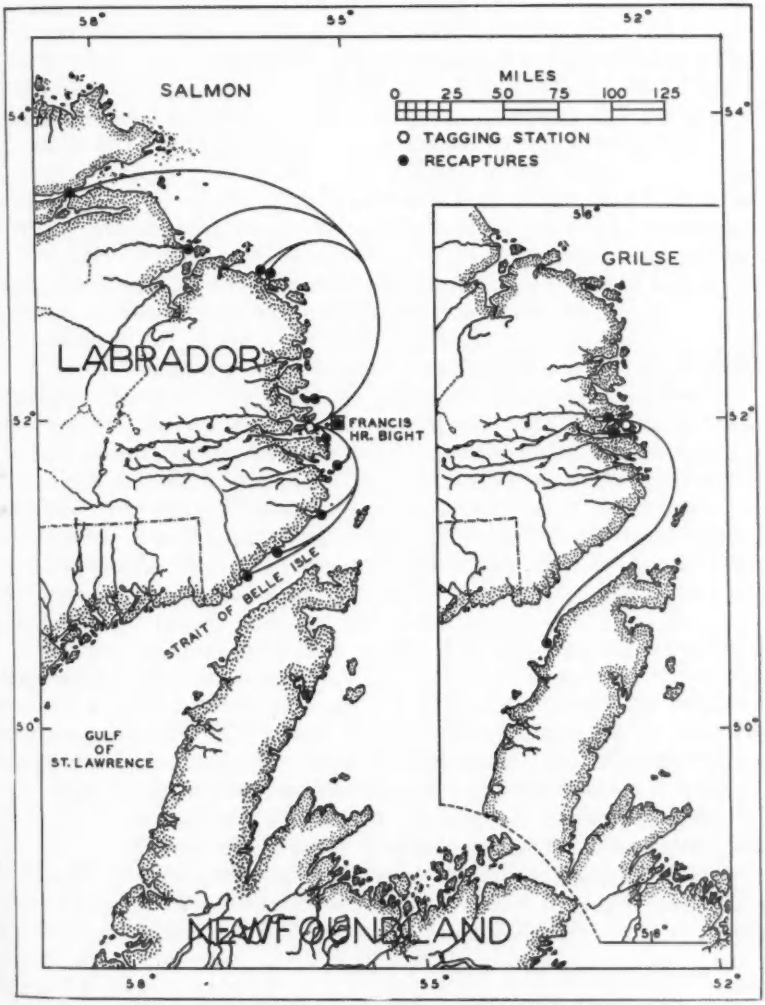

FIGURE 1. Distribution of salmon and grilse recaptured in 1950, the year of tagging.

1950) of the run was over before the beginning of tagging operations and most of the salmon caught in gill nets are not lively enough to tag.

As determined by scale reading, 94.6% of the tagged salmon spent 2 years in the sea, 1.4% spent 3 years, and 4.0% had previously spawned. This percentage sea-age distribution is fairly similar to that obtained by Blair (1943) for the southern section of Labrador in 1939. However, in 1939 a higher percentage (11.5) of the salmon had previously spawned which may suggest that exploitation has increased in this area.

Of the 74 salmon that were tagged, 14.9% were recaptured. All the recaptured fish were taken in commercial nets on the Labrador coast during the period July 3–28 in 1950, the year of tagging. The distribution of recaptured fish to the north of the tagging station was exactly equal to the distribution to the south (Fig. 1). This distribution conflicts with the idea of the fishermen in this area that the salmon are all moving north along the coast. The actual proportion moving north may be higher than these results indicate. The most northerly recapture was at the northern extremity of the commercial fishery and there would be little chance of getting tag returns from beyond that point. The salmon that went south did not go beyond the Strait of Belle Isle. The salmon tagged by Belding (1940) in 1938 at St. Anthony just south of the Strait of Belle Isle showed a much more extensive migration. As well as showing a movement to the Labrador coast, they were taken on the north shore of the Gulf of St. Lawrence and along the west coast of Newfoundland.

The proportion of 15% recaptured is low compared with 40% obtained at Bonavista in 1940. This difference in exploitation is perhaps fairly representative even though small numbers of salmon were tagged in both instances. The peak of the run is June 1 at Bonavista and June 30 at Francis Harbour Bight so the salmon striking the coast at Bonavista would likely be exposed to the fishery for a longer time. There was also a much greater spread in the distribution of the Bonavista recaptures and therefore there were more chances of these salmon being caught. Moreover, half of the Bonavista recaptures were from the east coast of Newfoundland where fishing effort would be considerably higher than on the Labrador coast. There is a fairly large salmon fishery in Labrador south of Francis Harbour Bight but it decreases north of that point. The northern limit of the fishery is in Hamilton Inlet at the head of which the northernmost recapture was taken (Fig. 1). Another factor favoring escape of salmon in Labrador from the commercial fishery is that there is not likely to be any delay in entering the rivers because of high water temperatures.

The average distance travelled by salmon going north was 98 miles and by those going south 47 miles. A salmon taken at Double Mer in Hamilton Inlet, north of the tagging station, travelled the greatest distance, namely 186 miles. The fastest rate of travel, 17 miles per day, was executed by a salmon recaptured in Sandy Hills Bay which is also north of the tagging station. Moreover, the average rate of travel was higher for salmon going north. A good correlation between distance travelled and rate of travel is evident in Table II.

The figures for average distance travelled and average and maximum rates of travel for salmon tagged at Francis Harbour Bight and recaptured in Labrador are remarkably similar to corresponding figures for salmon tagged at Bonavista and recaptured on the east coast of Newfoundland. The respective figures for the former are 72.1 miles, 8.2 miles per day, and 17.0 miles per day, and for the latter they are 64.0 miles, 8.0 miles per day, and 17.4 miles per day.

A few kelts are caught throughout the salmon run at Francis Harbour Bight. Three were tagged in 1950 and one was recaptured at the tagging station after an absence of 1 day.

TABLE II. The distance between tagging station and place of recapture, the interval between tagging and recapture, and the apparent rate of travel for recaptured salmon (excluding grilse and excluding one salmon taken at the tagging station).

Area	No.	Average distance, *miles*	Interval, *days*			Rate, *miles per day*		
			Av.	Min.	Max.	Av.	Min.	Max.
Labrador								
North of tagging sta.	5	97.6	9.6	2	21	10.2	5.6	17.0
South of tagging sta.	5	46.6	8.0	4	15	5.8	2.2	14.7
Total	10	72.1	8.8	2	21	8.2	2.2	17.0

TAGGED GRILSE

Although the grilse run in this area continues to the middle of August or later, the majority of the fishermen remove their nets during the first week of August. Because of stormy weather and numerous icebergs in 1950, the fishery was discontinued around the end of July by most of the fishermen. Of the 41 grilse tagged (Table I), only 3 (7.3%) were recaptured. They were taken during the period July 7–15 in 1950. Two were caught fairly close to the tagging station after a short absence, namely 2.5 and 9 miles distant after an absence of 3 and 4 days respectively. The third travelled south 117 miles to Current Island on the west coast of Newfoundland near the southern entrance to the Strait of Belle Isle.

The 7% return of tagged grilse is very low but it is about what should be expected because there is very little interest in the grilse fishery in Labrador. The main run of grilse occurs at a time when the fishermen are busy with the cod fishery and, coming as it does when the run of larger salmon is about over, it might be difficult to market the grilse. The majority of the gill nets are 6-inch mesh even though the minimum size of mesh permitted by regulation is 5 inches. The fishermen here prefer the 6-inch mesh net to the 5-inch because of the possible loss of some of the larger salmon in the latter. If traps could be used, a larger proportion of the grilse run would be caught, but apparently the current is too strong for traps to operate effectively.

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Salmon Tagging at Cape Charles, Labrador[1]

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ABSTRACT

Salmon from the commercial fishery at Cape Charles, southern Labrador, were tagged in 1948. During the short tagging period of June 30 to July 10, 35 salmon and 24 grilse were tagged. Due to delays in reaching Labrador the peak of the salmon run was missed, and it was difficult to get salmon in good condition for tagging because of storms. Salmon returns consisted of 5 taken in commercial gear in Labrador and 1 angled in a west coast Newfoundland river, giving a total recovery of 17.1%. Only 2, or 8.3%, of the tagged grilse were recaptured, both being caught in commercial gear in Labrador.

INTRODUCTION

Cape Charles is situated on the southern part of the Labrador coast about 40 miles from the northern end of Newfoundland (Fig. 1). It is a small settlement inhabited by fishermen during the summer months only. From June 30 to July 10, 1948, 35 salmon, 24 grilse, and 3 kelts were tagged within a radius of 1 mile of Cape Charles (Table I). The tagged fish were caught by commercial fishermen

Table I. Number of "salmon" (other than grilse) and of grilse tagged daily, and the approximate time of the runs as indicated by the fishermen.

Date, 1948	Number tagged	
	Salmon	Grilse
June 5	(first of run)	
" 25	(peak of run)	
" 30	5	
July 1	9	1 (first of run)
" 2	2	...
" 5	2	1
" 6	4	5
" 7	8	6
" 8	3	3
" 9	2	4
" 10	...	4
" 15	(end of run)	(peak of run)
" 31	...	(end of run)
Total	35	24

in 6-inch mesh gill nets. Although the fishermen here refer to these nets as traps, they are actually only gill nets with an extra large hook on the offshore end.

The usual time of the salmon run is June 5 to July 15 with the peak

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around June 25. The grilse run is several weeks later, July 1 to July 31 with the peak around July 15. Because of delays in reaching Labrador in time for the peak of the salmon run, it was difficult to get many salmon tagged. Also because of stormy weather experienced during the tagging period, most of the salmon were not lively enough to tag. The salmon fishery was considered to be fairly good by the local fishermen. The total catch of grilse is small compared with the salmon catch. Only grilse from the first part of the grilse run

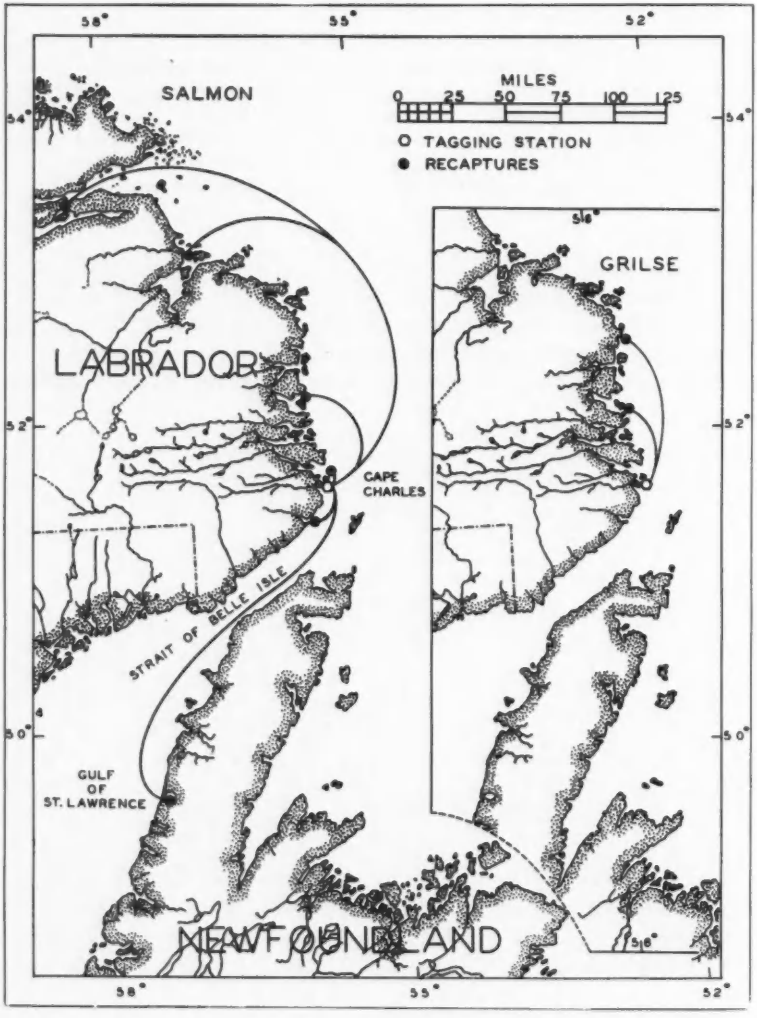

FIGURE 1. Distribution of salmon and grilse recaptured in 1948, the year of tagging.

were tagged since tagging operations had to be curtailed because of pressure of other work.

The nets are set in about equal numbers along the coast of the mainland and around several small islands. The fish are caught on both sides of the nets thus giving no indication of the direction of their destination. The best catches are made when the winds are onshore.

TAGGED SALMON
(excluding grilse)

Of the 35 salmon that were tagged, 6, or 17.1%, were recaptured and all of these were taken during the period July 1 to 29 of 1948, the year of tagging. There was one other return which is not included in the above. The tag was found in the stomach of a cod caught on August 29 at Cape Bauld, Newfoundland. The percentage returns are in fairly close agreement with those obtained in 1950 at Francis Harbour Bight (14.9%) which is about 25 miles north of Cape Charles (Blair, 1957).

The salmon tagged at Cape Charles were composed of 2-sea-year fish (97.1%) and previously spawned fish (2.9%). The proportion of previously spawned fish in the salmon tagged at Cape Charles in 1948 and in the salmon tagged at Francis Harbour Bight in 1950 was considerably lower than in the sample of salmon from southern Labrador in 1939 (Table II). From this it would appear that

TABLE II. Percentage sea age-composition of salmon sampled in southern Labrador in 1939, of salmon tagged at Cape Charles in 1948, and of salmon tagged at Francis Harbour Bight in 1950.

Place	Year	Sea age			Number of fish
		2 years	3 years	Previously spawned	
Southern Labrador	1939	87.9	0.6	11.5	348
Cape Charles	1948	97.1	0.0	2.9	35
Francis Harbour Bight	1950	94.6	1.4	4.0	74

exploitation has increased. Nevertheless, the rates of 15% at Francis Harbour Bight and 17% at Cape Charles as determined by tagging, although subject to error, should not be considered excessive. It is quite probable that at least some of these salmon are subjected to fishing pressure before reaching the Labrador coast since Belding's (1940) tagging at St. Anthony (northeast coast of Newfoundland) showed some dispersal to this coast.

Five of the recaptured salmon were caught in commercial nets in Labrador and one was angled on Portland Creek River on the west coast of Newfoundland, a distance of 168 miles from the tagging station (Fig. 1). The average distance travelled was 99 miles, and the interval between tagging and recapture was 3 to 10 days for the salmon taken in Labrador and 28 days for the salmon angled on Portland Creek River. A salmon taken at Rigolet, Labrador, went the greatest distance, 214 miles, and made the best time, 23.8 miles per day.

Three kelts were tagged but there were no recaptures. A few kelts are caught at the beginning of the salmon run and just an occasional one throughout the run.

TAGGED GRILSE

Only 2 of the 24 tagged grilse were recaptured giving a percentage recovery of 8.3. This low recovery is consistent with the low return of 7.3% for grilse tagged at Francis Harbour Bight which is in the same general area. The two recaptured grilse were caught in gill nets on the Labrador coast north of the tagging station, one at a distance of 40 miles and the other 66 miles (Fig. 1).

ACKNOWLEDGMENTS

Two fishermen, Rex Pye and William Pye, from Cape Charles were most co-operative. The tagging was done from their boats, and the crew members were always ready to help in any way. Technician Fred A. Day assisted in the tagging operations, and he and technician Alex. P. Cowan helped in preparing the paper.

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An Investigation of the Electrical "Spike" Potentials Produced by the Sea Lamprey (*Petromyzon marinus*) in the Water Surrounding the Head Region. II.[1,2]

By H. Kleerekoper and Kira Sibakin
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ABSTRACT

The rhythmically recurring spike potentials emitted by *Petromyzon marinus* are synchronous with the external respiratory movements but are not emitted through the branchial pores. Only total electrical shielding of the probranchial body eliminates these potentials from the water surrounding the animal. The principal area of emission is located in the eye region immediately cephalad of the first pair of branchial pores, in the area overlying the junction of the probranchial muscle and the hypobranchial branch of the parietalis. Probing of the skin with electrodes shows potentials of 1 millivolt on the surface of this area. These potentials are more than tenfold those recorded on any other part of the skin. It is assumed that the spike potentials described previously are emitted from the area defined above.

INTRODUCTION

In two previous communications (Kleerekoper and Sibakin, 1956a, 1956b) spike potentials generated by the sea lamprey, recorded from the water surrounding the head region, were described. The present communication deals with some of the results of experiments designed to provide further information on the localization of the emission of these potentials. In the two papers mentioned above the synchronous occurrence of the respiratory movements and the potentials recorded in the water was stressed. The previously reported observations (*l.c.*) demonstrated that the strongest electrical field occurs around the probranchial part of the body; in the experiments reported in the present paper, an effort was made to ascertain whether the movements of the water in and out of the branchial pores or the changes in the chemical composition of the water are directly responsible for the occurrence of the electrical potentials described earlier.

In addition to these experiments attempts were made, by electrical shielding and by direct probing with electrodes, to determine the locus or loci on the head from which the potentials are emitted.

METHODS AND RESULTS

The electronic and photographic equipment described in the two previous papers was used without modifications. All experiments were carried on inside a Faraday cage.

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[2]This research was done under contract with the Fisheries Research Board of Canada, at McMaster University, Hamilton, Ontario.

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EXPERIMENT No. 21

A lamprey was placed in a plastic tube, provided with electrodes (Kleerekoper and Sibakin, 1956a), so that only the probranchial part of the body was inside the tube. The remainder of the body, protruding from the tube, was partly supported in a shallow tray filled with water. Only the caudal part of the body was allowed to submerge while the branchial region was separated from the tray by means of a plastic sheet. By using one of the silver electrodes in the tube as a measuring electrode and the water in the tray as ground, the occurrence of electrical potentials emitted from the head region could be ascertained, without these potentials being affected by electrical phenomena which might be transmitted through the water by external respiratory movements, flow of water or chemical changes in the water brought about by respiration. To prevent water from leaking around the animal, out of the plastic tube, a collar of flexible material was placed around the animal where it protruded from the tube.

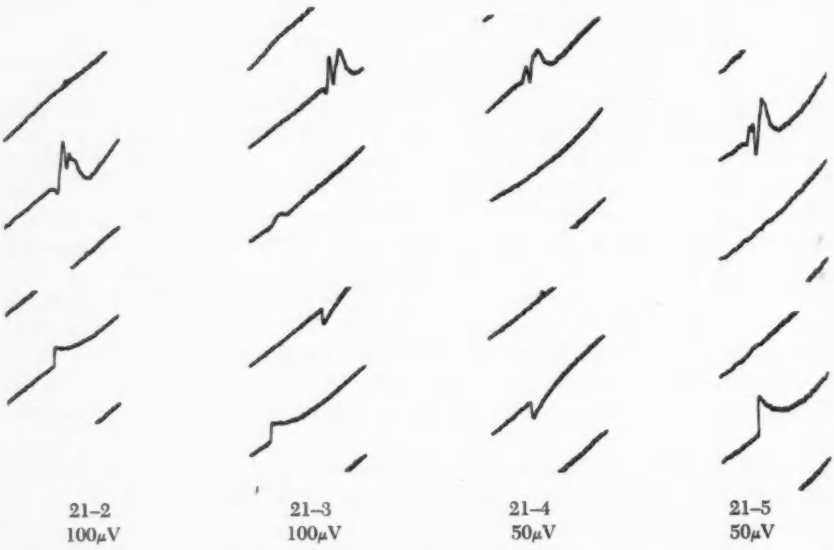

FIGURE 1. Spike potentials (upper records) recorded from the water surrounding the probranchial part of the body of *Petromyzon marinus*, with corresponding calibration signals in microvolts (lower records). The branchial and postbranchial parts of the body were suspended outside the plastic tube containing the measuring electrodes. The respiratory pouches were kept outside the water and could not directly affect the field measured inside the plastic tube. (Experiment 21—see the text).

Recording 21–2: measuring electrode 12 mm. in front of the edge of the mouth; spike potential 232 μV.
Recording 21–3: 225 mm. from mouth, potential 158 μV.
Recording 21–4: 475 mm. from mouth, potential 58 μV.
Recording 21–5: 550 mm. from mouth, potential 50 μV.

Measurements were made by means of the silver electrodes, at successively increasing distances from the animal. All the recordings of these measurements show the rhythmic occurrence of spike potentials as described earlier by the authors. Figure 1 represents a series of potentials recorded at increasing distances anteriorly from the edge of the mouth, i.e. away from the animal. A calibration signal accompanies the recording of each potential.

The recordings show the presence of rhythmically recurring potentials the values of which decrease with the distance of the measuring electrode from the animal. The highest potential measured was 232 μV, 12 mm. in front of the edge of the mouth; the lowest potential recorded was 50 μV at a distance of 550 mm. (Fig. 1, recordings 21–2 and 21–5). It is obvious that the absolute values of these measurements are of less importance than the relative values, since the former vary with experimental conditions.

The characteristics of the potentials, as shown in Figure 1, differ considerably from those recorded when the animal is completely contained in the plastic tube. The modulated spikes of Figure 1 are almost certainly due to emission by more than one source on the probranchial part of the body. The occurrence of rhythmic potentials under the experimental conditions described above indicates that the electrical pulses result neither from the flow of water into and from the branchial pouches nor from the chemical changes in that water as produced by respiration.

The synchronization of the recurrence of the potentials with the external respiratory movements requires probing of the possibility that respiratory muscle potentials directly produce the potentials recorded from the water. Experiment 21, described above, indicates that the emission of such muscle potentials into the water is not required to produce the electrical field observed. Further experiments must show whether such muscle potentials are the source of the electrical field recorded from the water or whether both phenomena receive synchronous impulses from a common centre such as the respiratory centre in the central nervous system.

Experiment No. 22

The experimental animal was partly covered with one or two pieces of flexible metallic tubing of the type used to shield wiring in electronic equipment against external electrical disturbances. Such tubing is woven of thin copper wire, is very flexible and its lumen can be easily adjusted to a wide range of diameters. In Experiment 22–1 only one piece of tubing was slipped over the head of the animal, so as to cover the eyes and the two anterior branchial pores. In Experiments 22–2 to 22–8, two pieces of tubing were used. One of these covered the posterior part of the body caudad of the 6th branchial pore. The second tube was used to cover the remainder of the body to varying degrees. In all but one case (22–2) the tubes were electrically connected with each other through a thin, insulated wire. Unlike the arrangement of Experiment 21, the whole lamprey was placed inside the plastic tube for measurements. The results of the observations are represented in Figure 2 and Table I.

TABLE I. Potentials recorded when the body of the lamprey was shielded by woven copper to varying degrees. (Experiment No. 22; see also Fig. 2.)

Recording No.	Number and position of shields	Value of potential in microvolts
22–1	one; eyes and 2 branchial pores covered	137
22–2	two, not connected by wire; for position of caudal tube see text. Anterior tube as 22–1	24
22–3	two, connected by wire; position as 22–2	10
22–4a	two, as above; anterior tube covering head completely	0
22–4b	two, as above; anterior 12 mm. of head exposed	15
22–5	two, as above; anterior 25 mm. of head exposed	19
22–6	two, as above; anterior 31 mm. of head exposed	19
22–7	two, as above; eyes and pineal eye exposed	35
22–8	two, as above; eyes, pineal eye and 3 anterior branchial pores exposed	55

The data obtained by these measurements are instructive. Shielding of only the head by means of a single shield (Experiment 22–1, Fig. 2) does not decrease the potential nearly as much as shielding with two shields. In the latter arrangement the caudal shield must be considered "ground" in relation to the second shield, which covers various parts of the probranchial part of the body. As long as only the probranchial shield is used the electrical field is but slightly affected (22–1). Application of the caudal shield, even without connecting both shields by a wire, reduces the potential by 82% (22–1: 137 μV; 22–2: 24 μV). It should be noticed that the two shields are still separated by four pairs of exposed branchial pores (pairs 3, 4, 5 and 6). The column of water separating the two shields acts here as a shunt. When the shields are connected by a thin insulated wire (22–3) the spike potentials are reduced to 10 μV. No potentials are recorded when the probranchial part of the body is completely covered by the shield as in 22–4a. The gradually increasing exposure of the head is accompanied by an increase in the potentials recorded (22–4b to 22–8).

The sharpest increase in this series of observations is from 22–6 to 22–7. In these the shielding of the eyes and pineal body is compared with the electrical exposure of these organs, the remainder of the body caudad of the eyes being shielded. The potentials increased from 19 to 35 μV, or by 85%. Further exposure of the body (22–8) including branchial pores 1, 2 and 3 resulted in a further but less marked increase in the spike potentials recorded (35 to 55 μV, or 57%).

There is thus little doubt that the emission of the electrical field by *Petromyzon* is localized in the probranchial and branchial parts of the body. The experiments reported above as well as those described previously (Kleerekoper and Sibakin *l.c.*) clearly point to the role of the eye region, including that of the pineal eye region, in this emission.

EXPERIMENT NO. 23

In this series attempts were made to determine the loci of emission by direct probing with an electrode on the skin of the animal. A steel needle, coated with plastic but for the tip, was placed on the skin of a lamprey which was kept on a plastic sheet in a shallow tray. Enough water was placed in the tray to cover the branchial pores. The reference electrode was submerged in the water of the

FIGURE 2. Spike potentials obtained from the water when part of the lamprey is covered by a woven-copper shield (Experiment 22; see Table I). The various degrees of shielding (as described in the text) are indicated by the numbers 22–1, 22–2, etc. The potential obtained is indicated by the upper trace above each number, while the calibration trace is below it, corresponding to either 50 or 100 microvolts.

tray. Probing with the measuring electrode on the skin was done along the pattern shown in Figure 3. The results are represented in Table II.

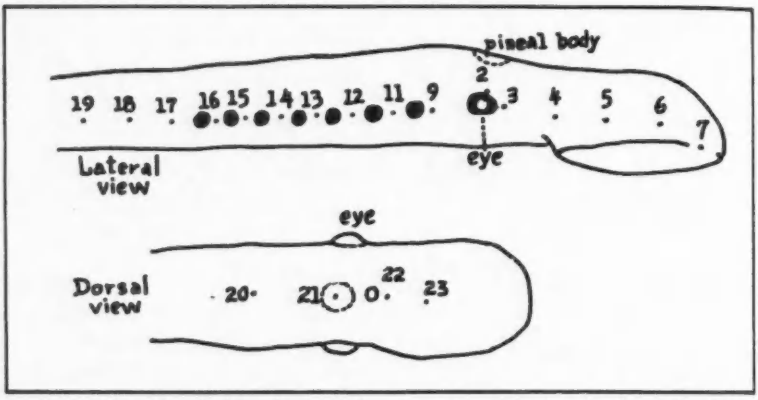

FIGURE 3. Positions (marked by dots) of the measuring electrode placed on the skin of the lamprey. The numbers refer to Table II—see the text. The large black circles are gill apertures; the open circle behind No. 22 is the nostril.

TABLE II. Potentials recorded by direct probing of the skin in various positions. (Experiment No. 23.)

Position of measuring electrode (see Fig. 3)	Average potential in microvolts (number of readings in brackets)
2	64 (6)
3	62 (5)
4	49 (5)
5	40 (5)
6	63 (5)
7	73 (5)
9	1040 (5)
11	89 (6)
12	88 (5)
13	100 (5)
14	90 (5)
15	70 (4)
16	72 (4)
17	0(<6)
18	16 (3)
20	73 (3)

In addition to the above measurements, others were made on the dorsal surface of the head, on the pineal body and on the ventral surface of the body. The highest potentials observed among the latter measurements were on the mid-ventral line a few millimetres caudad of the buccal rim (127 μV). Dorsally, midway between the eye and the pineal body, potentials of 108 μV could be registered. All other potentials, recorded from a variety of points, provided little additional information because of their low values (26–38 μV).

Among the data presented in Table II the high potential at locus 9 (1040 μV) is striking. This position is a few millimetres cephalad of the first branchial

pore and overlies the area where the probranchial muscle meets the hypobranchial branch of the parietalis. It should be recalled here that the experiment reported in Table I, recordings 22–6, 22–7 and 22–8, showed a marked increase in the potentials recorded from the water on removal of the shield covering this area of the animal.

CONCLUSIONS

The experimental data presented in this paper indicate that the spike potentials recorded from the water surrounding the head region of *Petromyzon marinus* are not emitted through the branchial pores. Total shielding of the probranchial body completely eliminates the potentials so that their emission must be sought there. Gradually increased exposure of this part of the body results in the reappearance and increase of the potentials. The latter is most striking on exposure of the first branchial pores and of the region of the eyes. Probing of the skin with an electrode further revealed an area, immediately anterior of the first branchial pore, with a potential more than ten times higher than any of the potentials recorded from other loci. Since this area overlies the junction of the probranchial muscle with the hypobranchial branch of the parietalis, and earlier experiments (Kleerekoper and Sibakin, 1956b) demonstrated that curare considerably depresses the spike potentials recorded from the water, it seems highly probable that these potentials result from muscle contractions in the area defined above. Further experiments will be done to define anatomically and histologically the area of emission.

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Mortalities Among Developing Trout and Salmon Ova Following Shock by Direct-Current Electrical Fishing Gear[1]

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ABSTRACT

Two units of direct-current fishing gear, providing terminal potentials of 550 and 150 volts, were used to give shocks of different severities to trout and salmon ova in various stages of development. The purpose of the tests was to establish precautionary measures to prevent damaging eggs when using similar apparatus, in waters of similar conductivity, in the vicinity of natural redds containing live eggs. High terminal voltage caused heavy losses among pre-eyed eggs, considerably fewer losses among eyed eggs, and no losses to eggs that were near hatching. There were no losses among eyed or pre-eyed eggs with low terminal voltage. Eggs that had been buried in the gravel of a stream apparently received some protection from electric shock. Salmon alevins were killed by prolonged severe shock, but not by a similar shock of shorter duration. The alevins showed greatly increased activity and swam about sporadically when in the electric field, but did not exhibit galvanotropic responses of a directional character.

INTRODUCTION

In the course of an investigation of the interspecific relationship of the American eel (*Anguilla bostoniensis* (LeSueur)) and young Atlantic salmon (*Salmo salar* Linnaeus) in New Brunswick streams, it was planned to use direct-current (d-c.) electrofishing equipment in the vicinity of salmon redds. Because an estimate of the hatch from the eggs was desired, it was felt that tests should first be conducted to determine whether fish embryos would be harmed or killed by shocks of different severities that could be given with the apparatus. This paper describes the results of such tests, which were carried out during the winter of 1950–51.

A few preliminary tests were made in a small stream (Holme's Brook) at Petitcodiac, N.B., using eggs and milt from a pair of sea-run salmon captured in the Pollett River. The remaining, and greater number, of tests were carried out at the Federal Department of Fisheries hatchery at Saint John, N.B., where salmon and trout (*Salvelinus fontinalis* (Mitchill)) eggs in various stages of development were available, and where the facilities for treating the eggs, and for retaining them for subsequent observation, were suitable.

Hayes and Armstrong (1942), and Battle (1944) have observed that developing trout and salmon ova are highly susceptible to adverse conditions; first, following early cleavage until the "eyed" stage is reached, and, second, just prior to hatching. In hatchery operations it is customary to plant or transport salmon

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and trout eggs either during the period up to about 36 hours after fertilization, or after they have reached the eyed condition.

Mortalities occurring during the pre-eyed stage are believed to result from rupture of the vitelline membrane, and they have been induced experimentally by a variety of stimuli, including natural and electric light, agitation, pressure, heat, cold, and electric currents (Hayes, 1949; Affleck, 1953). The subsequent safe period, according to Hayes, begins when the vitelline membrane over the yolk is replaced by a protective layer of cells. This occurs at about the time the embryo has reached the eyed stage.

Hayes (1930) noted that in the early critical period the sign of death was a general whitening of the egg, which took place in the yolk. Mortalities occurring just prior to hatching were apparently due to failure of sufficient oxygen to reach the embryo through the egg capsule (Hayes, 1949), and in these instances it was the embryo and not the yolk that first turned white.

ELECTRICAL APPARATUS

Two d-c. generators were used, the larger delivering in open circuit approximately 550 volts, and the smaller, 150 volts. The two machines and their accessory parts have been described by Smith and Elson (1950). The positive, or fishing, electrodes were of a shape somewhat like a tennis racquet with an extra long handle. They could be dipped into the water at the required depth and distance from the egg samples, while a switch in the handles of the electrodes made it possible to deliver shocks of required durations. The negative electrode for each generator consisted of a small square of copper screening (6 sq. ft. or 0.5 sq. m.), which was grounded to the bottom of the stream (or trough). In these tests it was placed well away from both the positive electrode and the egg samples.

METHODS

The Petitcodiac eggs were placed in perforated celluloid cylinders (of the type used to hold a bar of soap, but with many additional perforations), which were then set on the bottom of a stream in 6 to 8 inches (15 to 20 cm.) of water. One set of eggs before shocking was buried under about 8 inches (20 cm.) of gravel in the stream bed to simulate conditions in a redd.

At the Saint John hatchery, samples of eggs were placed in open, shallow glass Petri dishes, which were then set on the bottom of concrete troughs in which water ran at a depth of approximately 8 inches (20 cm.). These troughs were out of doors. After shocking, the eggs were returned to the indoor wooden troughs from which they had been taken, and were held there for subsequent observation. (The Petri dishes were approximately 4 inches (10 cm.) in diameter, and ¼ inch (0.6 cm.) deep. The concrete troughs were roughly 4 feet (1.2 m.) wide, and more than 30 feet (9 m.) long.

Fifty eggs per sample were used in the Petitcodiac tests; 20 per sample in Series 1 and 2, and 50 per sample in Series 3, at the Saint John hatchery. Some of

the controls were divided into two identical lots of either 20 or 50 eggs per sample; and some of the treated samples had one or two fewer or extra eggs.

Samples of eggs as controls were handled in as similar a manner as possible to treated eggs, exclusive of shocking. In the case of the Saint John tests this involved counting them (from the indoor troughs) into the Petri dishes, taking them to the outdoor troughs, and later returning them to the indoor troughs for rearing and observation. This amount of handling was considerable, and must have killed eggs, since losses among controls of eggs in the pre-eyed state were heavy, and were much greater than among non-experimental eggs being raised under normal hatchery conditions.

Variation in the severity of shock was achieved by changing either the distance of the electrode from the eggs, the duration of the current flow, or both. The voltage delivered under load was held approximately constant for each of the two machines used.

In addition to trout and salmon eggs, shocks of several severities were also administered to recently hatched salmon alevins. This was done to determine whether they were harmed or killed by the shocks, and also to discover whether they oriented themselves or swam in relation to the direction of the current flow. Depending upon their behaviour within the electric field, it might prove feasible to use d-c. fishing gear to effect the emergence of alevins from redds, so that they could be sampled or counted. Twenty alevins were used in each sample including controls.

The Petitcodiac tests were carried out on November 27–28, 1950, and the Saint John hatchery tests during December 11–12, 1950, and later during February 12–13, 1951. Inspections of eggs were made at intervals over a period of about 24 hours after treatment, after which the writer was able to visit the hatchery only at relatively long intervals during the winter. Arrangements were therefore made for personnel of the hatchery to examine the eggs about once a week, at which time they recorded the number of dead eggs in each sample, and removed them from the retaining compartments.

DETERMINATION OF EFFECT

Frequently the sign of death in salmon or trout eggs is the appearance of an opaque, white spot which spreads until finally the whole egg looks a cloudy white. When the recently fertilized Petitcodiac eggs (in early cleavage) were shocked, the white spot appeared in from 5 to 60 minutes after shocking. In such cases the occurrence of the white spot was a convenient means of assessing effect through recognition of the death of the egg. With eggs that had proceeded further in development, however, the white spot did not usually appear until many hours, or even days, after the embryo had died. In such instances, although the death of the embryo could still be used as the criterion of effect, when finally identified, it was not possible to time its occurrence accurately. For these reasons most of the eggs used in these tests were retained in the hatchery until such time as they had hatched, or were obviously dead.

RESULTS OF THE PETITCODIAC STREAM TESTS

Tests were made with the Wolf machine delivering in closed circuit 550 volts at 1.7 amperes. Eggs used were recently fertilized salmon eggs, some pre-cleavage, and some in early cleavage. Results are shown in Table I.

TABLE I. Results of Petitcodiac tests. In Test 3, eggs were buried under about 8 inches (20 cm.) of gravel. All shocks were administered from a distance of 6 inches (15 cm.). Each "b" test is a replicate of each "a" test.

Number of test	Duration of incubation	Development	Duration of of shock	Number of of eggs used	Mortality after 1 hour
	hours		*seconds*		%
1	5–6	pre-cleavage	25	50	0
2	5–6	pre-cleavage	120	48	81
3	5–6	pre-cleavage	120	50	10
4a	28–30	early-cleavage	30	50	90
4b	28–30	early-cleavage	30	51	97
5a	28–30	early-cleavage	60	50	100
5b	28–30	early-cleavage	60	50	100
6a	28–30	early-cleavage	120	50	100
6b	28–30	early-cleavage	120	50	100
Control	5–6	pre-cleavage	..	50	0
Control	28–30	early-cleavage	..	50	0

The appearance of the white spot on many eggs of several tests in less than an hour after shocking (and in the case of several eggs of Test 2 within 10 minutes or less) made it possible to determine a harmful effect and death.

There were no losses among the controls. Pre-cleavage eggs were killed by prolonged shock of 120 seconds duration, but not by the less severe treatment of 25 seconds duration. Early-cleavage eggs, on the other hand, suffered total or almost total losses within the hour, from shocks of 30, 60 and 120 seconds duration.

The pre-cleavage eggs that had been buried under 8 inches (20 cm.) of gravel (Test 3) suffered considerably fewer losses than similar but exposed eggs given a shock of equal severity (Test 2).

RESULTS OF THE SAINT JOHN HATCHERY TESTS

Eggs used included:

Type A. Trout, early cleavage, incubation–6 days.
Type B. Trout, late cleavage; incubation–27 days.
Type C. Trout, late-eyed; incubation–44 days; about 60 somites.
Type D. Salmon, eyed; incubation–27 days; about 40 somites.
Type E. Salmon, body almost completely formed.
Type F. Trout, near to hatching.
Type G. Trout, early-eyed.
Type H. Trout, body almost completely formed.

SERIES I (TABLES II–IV)

Tests were made on December 11–12, 1950, using eggs of Types A, B, C and D; and administering shocks of 550 volts at 1.7 amperes with the Wolf machine.

TABLE II. Series 1. Percentage hatch of 4 types of eggs after shocks at various distances and of various durations. 550 v.; 1.7 amp. (At the

TABLE II. Series 1. Percentage hatch of 4 types of eggs after shocks at various distances and of various durations. 550 v.; 1.7 amp. (At the Saint John hatchery.)

Distance—*feet* (*m.*):	1(0.3)				3(0.9)				6(1.8)				12(3.7)			
Egg type:	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
Duration of shock (*seconds*)	Percentage hatch															
30	0	0	75.0	70.0	0	0	47.4	35.0	0	0	95.0	45.0	—	—	—	—
60	0	0	55.6	0	0	0	75.0	65.0	0	0	65.0	50.0	0	0	95.0	75.0
180	0	0	78.4	0	0	10.0	90.0	90.0	0	0	70.0	90.0	—	—	—	—
300	—	—	—	—	—	—	—	—	—	—	—	—	0	15.0	76.2	80.0

TABLE III. Series 1. Time to approximately 50% mortalities among 4 types of eggs after shocks at various distances and of various durations. 550 v.; 1.7 amp. (h = hours; d = days; * = final loss less than 50%.) (At the Saint John hatchery.)

Distance—*feet* (*m.*):	1(0.3)				3(0.9)				6(1.8)				12(3.7)				Controls			
Egg type:	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
Duration of shock (*seconds*)	Time to 50% mortalities																			
30	24 h	<24 h	*	*	<24 h	<24 h	18 d	46 d	24 h	<24 h	*	18 d	—	—	—	—				
60	20 h	24 h	*	20 h	>24 h	24 h	*	*	8 d	>48 h	*	32 d	>48 h	>48 h	*	*				
180	<1 h	<1 h	*	1.5 h	9 d	12 d	*	*	9 d	<48 h	*	*	—	—	—	—	26 d	56 d	*	
300	—	—	—	—	—	—	—	—	—	—	—	—	8 d	8 d	*	*				

TABLE IV. Series 1. Percentage losses among treated eggs and controls up to 24 hours after electrical shock. 550 v.; 1.7 amp. (At the Saint John hatchery.)

Distance—*feet* (*m.*):	1(0.3)				3(0.9)				6(1.8)				12(3.7)				Controls			
Egg type:	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
Duration of shock (*seconds*)	Percentage losses																			
30	44.4	80.0	0.0	5.0	55.0	55.0	0.0	5.0	45.0	60.0	0.0	10.0	—	—	—	—				
60	55.6	73.7	5.6	50.0	5.0	50.0	5.0	0.0	10.0	42.1	0.0	10.0	10.0	35.0	0.0	10.0				
180	100.0	95.0	5.3	100.0	10.0	5.0	5.0	5.0	15.0	33.3	0.0	0.0	—	—	—	—	0.0	5.0	0.0	0.0
300	—	—	—	—	—	—	—	—	—	—	—	—	0.0	10.0	9.5	0.0				

TYPE A EGGS

No trout eggs in early cleavage hatched after electrical shock (Table II). Among controls of these eggs there was a 50% loss within 26 days; the remainder hatched (Table III).

Considerable variation occurred in the apparent rate of death, as indicated by the discovery of eggs with white spots. Inspections for dead eggs were made at intervals during the first 24 hours after treatment; Table IV shows the percentage losses (i.e. eggs with visible white spots) in the different samples as at 24 hours, approximately, after shock. There is no clear indication among Type A eggs that mortalities tended to increase, or to become apparent earlier, the more severe the shock given (Tables III and IV). However, as Table IV indicates, if duration of shock is ignored altogether, more eggs showed opaqueness within 24 hours among those shocked at 1 foot than among those shocked at greater distances.

Mortalities among controls were high and must be presumed to be due to handling since they were considerably greater than occurred among the normal hatchery eggs. However, since about 50% did hatch, as compared with no hatchings among the treated eggs, it is concluded that the trout eggs in early cleavage did suffer directly from the electrical shocks they received.

TYPE B EGGS

In general, losses among late-cleavage trout eggs were similar to those among Type A, early-cleavage trout eggs. A few of the Type B eggs which were given shocks did hatch (10% of those shocked for 180 sec. at 3 ft.) but all the remainder died (Table II). There was a 25% loss within 26 days among Type B control and a 50% loss within 56 days (Table III); 40% of the controls finally hatched.

Again, as with Type A eggs, losses became apparent sooner among eggs shocked at 1 foot (0.3 m.) than at greater distances (Tables III and IV), but otherwise a definite relationship between severity of shock and mortality cannot be determined for Type B eggs.

TYPE C EGGS

The hatch among late-eyed trout eggs was 50% or higher in 10 of 11 cases and 47.4% in the remaining sample (Table II). There were no losses among the controls and all hatched. Thus, although late-eyed trout eggs were evidently susceptible to damage by severe d-c. shock, losses were lighter than among Types A and B eggs (in early and late cleavage, respectively).

Variation in mortality due to differences in severity of shock could not be determined (Tables III and IV).

TYPE D EGGS

Among the eyed salmon eggs given shocks the percentage hatch was 50% or greater in 7 of 11 cases (Table II). Ninety-five per cent of the controls hatched. In general, the results for eyed salmon eggs were similar to those for late-eyed trout eggs (Type C), and some mortality directly due to electric shock is

indicated (Tables III and IV), particularly in the case of the severe shocks of 60 and 180 seconds at 1 foot (Table III).

SERIES 2 (TABLE V)

Tests were made on December 10–11, 1950, using eggs of types A, B, C and D; and administering shocks of 150 volts at 0.6 ampere with the small generator.

Losses among controls were very similar to those among treated eggs, with only one important exception—Type A eggs (early cleavage trout) at 3 feet (0.9 m.) for 60 seconds (Table V). There is no clear indication, therefore, that mortalities among the shocked eggs resulted directly from the electric treatment.

The eggs were inspected at intervals during the first 24 hours after shock. Up to 24 hours the losses amounted to 1 egg each in 3 treated and 2 control samples. There were therefore no significant differences between the effects of different kinds of treatment.

SERIES 3 (TABLES VI–IX)

Tests were made on February 12–13, 1951, using eggs of Types E, F, G and H and administering shocks of 575 volts at approximately 1.5 amperes.

These eggs were observed over a period of 25 days after shocking; it was not possible to keep them under observation longer. By this time hatching had begun to take place among the more advanced eggs of Type F, but not among the others.

TYPE E EGGS (TABLE VI)

Losses among treated salmon eggs (body almost completely formed) were extremely low and cannot be ascribed definitely to electric shock. Among controls the loss amounted to 1.0% during the 25 days.

TABLE VI. Series 3. Percentage losses among Type E eggs during 25 days after electric shock. 575 v.; 1.5 amp. (At the Saint John hatchery.)

Distance—*feet* (*m.*)	1(0.3)	3(0.9)	6(1.8)	12(3.7)	21(6.4)	Control
Duration of shock (*seconds*)	Percentage losses					
60	2.0	0.0	2.0	2.0	0.0	1.0
300	0.0	0.0	2.0	2.0	0.0	

TYPE F EGGS (TABLE VII)

Losses among treated trout eggs (near to hatching) were extremely low, and again, cannot be attributed definitely to the shock they received. Only 2.0% of the control eggs died. Among both treated eggs and controls all but a few eggs had hatched by the 25th day after treatment.

TABLE VII. Series 3. Percentage losses among Type F eggs during 25 days after electric shock. 575 v.; 1.5 amp. (At the Saint John hatchery.)

Distance—*feet* (*m.*)	1(0.3)	3(0.9)	6(1.8)	12(3.7)	21(6.4)	Controls
Duration of shock (*seconds*)	Percentage losses					
60	2.0	0.0	0.0	0.0	4.0	2.0
300	0.0	0.0	0.0	0.0	2.0	

TABLE V. Series 2. Percentage hatch of 4 types of eggs after shocks at various distances and of various durations. 150 v.; 0.6 amp. (At the Saint John hatchery.)

Distance—*feet* (*m.*):	1(0.3)				3(0.9)				6(1.8)				Controls			
Egg type:	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
Duration of shock (*seconds*)	Percentage hatch															
60	55.0	75.0	85.0	85.0	0	55.0	94.7	85.0	40.0	52.6	65.0	90.0	50.0	40.0	100.0	90.0
180	55.0	55.0	90.0	100.0	35.0	70.0	95.0	100.0	30.0	35.0	95.0	95.0				

TYPE G EGGS (TABLE VIII)

With the exception of the 60 seconds shock at 12 feet (3.7 m.), the losses among the treated eggs (trout, early-eyed) were distinctly higher than among the controls in which the loss amounted to only 1.0%. Although mortality resulting from electric shock is indicated, it is not possible to distinguish clearly between shocks of different severity.

TABLE VIII. Series 3. Percentage losses among Type G eggs during 25 days after electric shock. 575 v.; 1.5 amp. (At the Saint John hatchery.)

Distance—*feet* (*m.*):	1(0.3)	3(0.9)	6(1.8)	12(3.7)	21(6.4)	Controls
Duration of shock (*seconds*)	Percentage losses					
60	5.9	2.7	7.8	0	6.3	1.0
300	14.0	2.0	10.4	4.0	2.0	

TYPE H EGGS (TABLE IX)

Percentage losses among treated eggs were, in general, similar to those among controls. However, there is some indication of possible harmful effect from electric shock upon these trout eggs (with body almost completely formed), in the fact that in 4 of 5 cases losses among eggs shocked for 300 seconds were greater than among those shocked for 60 seconds.

TABLE IX. Series 3. Percentage losses among Type H eggs during 25 days after electric shock. 575 v.; 1.5 amp. (At the Saint John hatchery.)

Distance—*feet* (*m.*):	1(0.3)	3(0.9)	6(1.8)	12(3.7)	21(6.4)	Controls
Duration of shock (*seconds*)	Percentage losses					
60	6.0	2.1	10.0	2.1	5.8	5.1
300	7.8	3.8	8.0	5.9	15.7	

SERIES 4 (TABLE X)

Salmon alevins were given d-c. shocks of 575 volts at 1.5 amperes (Wolf machine) for 60 seconds at 1 and 3 feet (0.3 and 0.9 m.), and for 300 seconds at the same distances.

The only losses that occurred among the alevins were those that resulted from the 300 seconds shock at 1 foot (0.3 m.); all were found dead on the 6th day after shock (but were alive up to at least 1 hour after treatment).

In each test the response of the alevins to the electric shock was immediate. They contorted violently and swam sporadically about the container. None was seen to orient in relation to the direction of the source of the current, nor to move directly toward, or away from, the positive electrode. After the first few seconds of the shock the alevins usually ceased their movements briefly but this was followed by further swimming and contortion, then again a brief period of rest.

TABLE X. Percentage losses among salmon alevins given D.C. electric shocks of 575 v. at 1.5 amp. at two distances and for two durations. (At the Saint John hatchery.)

Distance—*feet* (*m.*):	1(0.3)	3(0.9)	Controls
Duration of shock (*seconds*)	Percentage losses		
60	0	0	0
300	100.0	0	

SUMMARY AND DISCUSSION

With high terminal potential (550 v.) pre-cleavage salmon eggs (Petitcodiac eggs) were killed by very severe d-c. shock. Salmon eggs in early cleavage (Petitcodiac eggs) suffered total mortalities from shocks of all severities administered. Losses among eyed trout and salmon eggs (Types C, D, E, F, G, H) were much lighter than were losses among trout eggs in the pre-eyed condition (Types A, B). Among eggs of both trout and salmon that were well advanced in development (Types E, F, H), including some close to hatching (Type F), no losses could be attributed directly to electric shock.

With low terminal potential (150 v.) no losses resulting directly from electric shock could be determined, among either eyed or pre-eyed eggs (Types A, B, C, D).

Salmon alevins that were subjected to very severe electric shock (550 v. 300 sec., at 1 ft.) were all killed, but those that experienced a similar shock of shorter duration were apparently unharmed. In the electrical field the alevins contorted their bodies and made abrupt and disorganized swimming movements, interspersed with brief periods of rest. They did not exhibit a distinctly directional galvanotropic response.

The apparent effect of burying eggs under a layer of gravel was to give them some protection from the electric shock. Salmon eggs in pre-cleavage were used and were buried in a stream bed under about 8 inches (20 cm.) of gravel. Atlantic salmon usually bury their eggs a few inches deeper, so that eggs in a natural redd might receive even more protection from the current of d-c. electrical fishing gear. This aspect of the problem needs further study, particularly with eggs in other stages of development.

The general results of the tests described herein suggest that the effects of shock from the d-c. fishing gear were similar to those described by earlier workers using other kinds of stimuli; i.e., developing fish eggs are highly susceptible to adverse conditions during the period following early cleavage until the eyed stage is reached. This initial period ends (Hayes, 1949) when the vitelline membrane over the yolk is replaced by a protective layer of cells (which occurs at about the time the embryo has "eyed"). Hayes also describes as critical a period just prior to hatching, if there is a failure of sufficient oxygen to reach the embryo through the egg capsule. Since, in these tests, no losses directly attributable to the electric shock occurred among eggs close to hatching, it is concluded that the

stimuli given did not affect either the oxygen demands of the embryos, or their ability to take up oxygen, seriously enough to kill them.

In tests of severities similar to those given to eggs with embryos close to hatching, salmon alevins were not killed by electric shock. Their ability to respire, then, could not have been impaired too seriously. However, all alevins were killed by a shock, which in the first instance did not kill, whose duration was continued much longer (killed when for 300 sec., but not when for 60 sec.). The alevins that finally died were alive and had therefore been respiring up to at least 1 hour after treatment; they were not observed again until 6 days later when all were found dead. A delayed effect is thus indicated but what the final cause of death was cannot be determined.

Variation in response due to differences in severity of shock was shown but in most cases it was not possible to identify clearly differences in mortalities associated with variation in either distance from source or duration of stimulus. Losses from electric shock did occur with the use of large terminal potential (550 v.), but not with low terminal potential (150 v.) for similar distances and durations. In a number of instances losses of eggs were greater when shocks were delivered from a distance of 1 foot (0.3 m.) than at greater distances. Finally, salmon alevins were killed by a 300-second shock but not by a 60-second shock otherwise identical.

The difficulty that occurred in most cases of distinguishing between the effects of shocks given at different distances, or for different durations, partly resulted from the fact that losses due to handling alone were heavy. During the critical period of development described above, losses occurred among controls as well as among treated eggs. Since losses among the eggs being raised normally in the hatchery were much lighter than among controls, the handling of the experimental eggs must have been harmful. (The actual percentage loss in the hatchery among eggs of types used in the experiments was not ascertained; but they were relatively light and presumably were normal for hatchery operations.) Another factor contributing to the difficulty of distinguishing between results from different severities of shock was that after the first 24 hours or so following shock, eggs could be inspected only at 7- to 10-day intervals, and by the writer himself only at even longer intervals. More frequent inspections would have made it possible to record the time of appearance of dead eggs more accurately.

The purpose of these tests was to establish certain precautions to be taken when using these and similar apparatus in streams in the vicinity of redds containing live salmon or trout eggs. Since the electrical resistance of natural waters varies, and, too, since electrical conductance changes with temperature, the following comments apply to waters of similar electrical conductivity. Direct-current fishing apparatus with electrical output similar to the Wolf machine (terminal potential 550 v.) should not be used too close to redds, particularly if the eggs in them are in the pre-eyed condition. Considering that the eggs receive some protection by being buried in the gravel, a safe distance for brief periods might be 1 or 2 feet (0.3 or 0.9 m.). Until more has been learned of this apparent protection, a useful precaution might be not to use the electrode directly on or

even over the redds. Voltages such as were provided by the smaller machine (terminal potential 150 v.) are probably quite safe, but again, caution might be used when operated over a redd.

Since alevins were killed by prolonged severe shock, care should be exercised when using high terminal voltage. Although in these tests alevins did not respond with directional galvanotropic behaviour, their activity was increased considerably and they did swim about. Thus it might still be possible to use direct-current stimuli to effect their emergence from the gravel so that they could be sampled or enumerated.

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Some Factors Influencing the Distribution of Pelagic Copepods in the Queen Charlotte Islands Area[1,2]

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ABSTRACT

The distribution of certain copepod species of the north coast of British Columbia suggests that breeding is restricted to limited regions of well-defined temperature and salinity characteristics. Currents are responsible for the spread of juveniles and adults from these areas. Probable water circulation patterns in the vicinity of the Queen Charlotte Islands are inferred from the plankton collections.

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INTRODUCTION

During the summer of 1953, the waters adjacent to the Queen Charlotte Islands were surveyed in the C.G.M.V. *Cancolim* under the scientific direction of Dr. R. F. Scagel and Mr. F. G. Barber and the sponsorship of the Defence Research Board of Canada. In the area where plankton was sampled, physical and chemical data were also taken, thus permitting a study of the relationship between the distribution of plankton copepods and the oceanographic conditions in the area.

The plankton was sampled mostly by vertical towing from a known depth to the surface. Since this method in itself gives no indication of the vertical distribution of the copepods, an approximation of the depth distribution was obtained by comparisons of the contents of samples taken from different depths. The copepods found in most of the samples, including those taken from the shallow water, were considered as surface species while those taken only from the deeper water were considered as sub-surface or deep water forms depending

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on the depth from which the sample was taken. This analysis provided a rough approximation of the vertical distributions of the species of copepods necessary for a study of the factors influencing horizontal distribution.

The regions in which the various species were abundant and present in all stages were considered to be breeding areas. Some of these localities could be characterized by certain temperature and salinity conditions. Where the copepods were rare, however, and present in only a few stages, they were considered to be scattered from a breeding area. As this scattering could only be due to water movements, it was possible to suggest the directions of the currents in several areas where dispersal could be detected.

METHODS AND MATERIALS

The data and samples considered in this study were taken in the Queen Charlotte Islands Area between July 18 and August 8. The physical and chemical data have been presented in the Data Report No. 4 by the Institute of Oceanography at the University of British Columbia. Plankton samples were taken at the stations indicated in Figure 1. Most of these samples were obtained with vertical hauls from a known depth to the surface. At all the stations indicated one deep haul was taken from near the bottom to the surface with a 30-inch diameter net having a No. 10 mesh. At about half of these stations additional supplementary hauls were taken from 1, 3 or 14 meters to the surface. A 10-inch diameter net was used for these hauls.

The results of this sampling were not considered quantitatively accurate for two reasons. An indication of faulty filtration was noted at some stations (69, 72, 73, 86, 87, 112, 114, 115, 116, 128) where *Microsetella norvegica* and *Acartia clausi* were captured in the supplementary hauls but not in the deep hauls. This suggested that the net used for the deep haul was clogged when it reached the surface and failed to capture species occurring near the surface. It was suspected that clogging also caused ineffective sampling even where no qualitative discrepancies were evident. Also, no duplicate samples from the deep water were taken. As several workers (Barnes and Marshall, 1951; Hardy and Günther, 1935) have found that the patchy distribution of plankton can cause considerable variability between duplicate samples, the samples taken in this survey are not assumed to be completely representative. Only gross differences in the numbers of animals are considered significant. "Rare" refers to, at the most, one copepod in a liter of sample, "few" means up to 10, "common" means up to 25, and "abundant" means up to 50 per liter. These figures refer to the maximum numbers of animals in each category. Rare, for instance, usually refers to much fewer than one per liter.

In Masset Inlet most of the samples were taken from water pumped through a hose from a discrete depth. The end of the hose was attached to an anchored wire and lowered to a known depth. Water was then pumped to the surface and strained through a plankton net. Because the accuracy of this method is unknown, the same very approximate categories mentioned above are used to designate the concentration of copepods.

The species of copepods were determined by reference mostly to Davis (1949). Giesbrecht (1892), Sars (1903) and Esterly (1905, 1911, 1924) were also consulted. The species of a few genera occurring in the deep water were not determined.

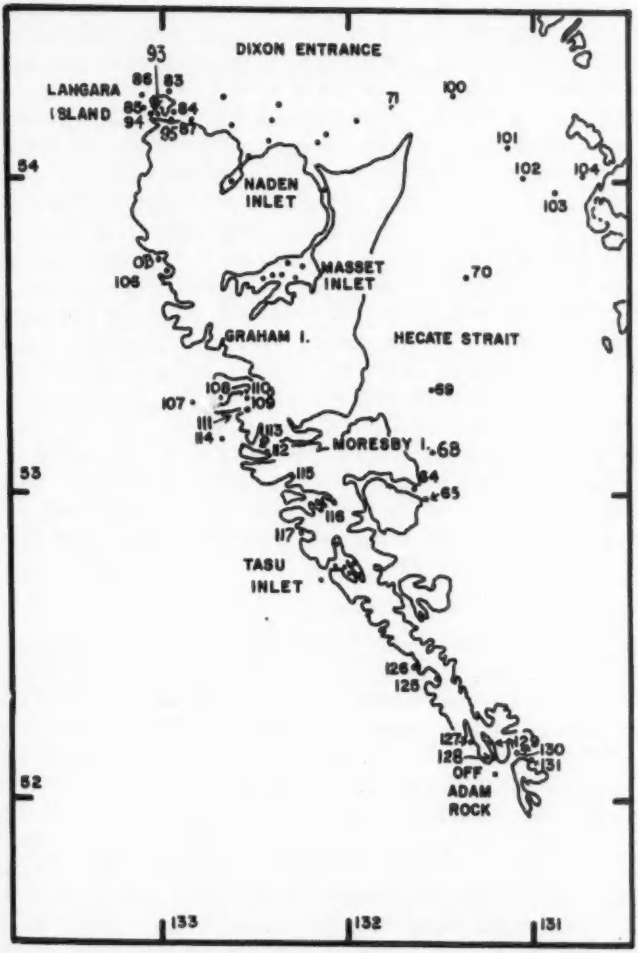

FIG. 1. Plankton stations taken adjacent to the Queen Charlotte Islands by the *Cancolim II* during the summer of 1953. (For the station numbers in Tasu Inlet see Fig. 16; for Dixon Entrance see Fig. 20; for Masset Inlet see Fig. 24.)

VERTICAL DISTRIBUTION

The vertical distribution of the copepod species became apparent when the contents of the hauls taken from different depths were compared. Although it

is well known that the various species occur at different depths, the information on these vertical ranges given by some authors was not thought to be precise enough (Davis, 1949; Giesbrecht, 1892; Wilson, 1953). Some information (Furihasi, 1953) was detailed but was not considered applicable to the Queen Charlotte Islands area. In order to obtain some idea of the vertical distribution, the depths of the hauls in which they were captured were considered. The hauls were arranged according to depth. Species occurring near the surface could have been captured by the shallow hauls as well as by the deep hauls while only the deeper hauls would capture species living below the surface waters.

The upper limits of the species living near the surface could be fairly well determined by comparing the results of the supplementary haul with those of the deep haul. If a species were common in the supplementary haul and in the deep haul, it was assumed to be living almost entirely at the surface, while a species absent in the surface haul but present in the deep haul presumably occurred somewhere below the depth of the surface haul.

Some species, however, lived well below the depths of the supplementary hauls. In localities where deeper stations were close together, it was possible to estimate the approximate depth where the uppermost individuals occurred by comparing the contents of adjacent stations. If a species, occurring in a particular deep haul, were absent from an adjacent more shallow haul, the upper limit of its vertical distribution was taken to be the depth of the more shallow haul. Although the results of the comparisons of adjacent stations appear adequate, the dependency of the upper limits on the depths of the adjacent hauls probably involves error. These results, however, seem consistent and have yielded some valuable information.

Horizontal Distribution

In the discussion, horizontal distributions have been depicted on small maps on which the occurrence of the species and its relative abundance are indicated by circles. The distributions are considered in the light of temperature and salinity data as well as geographical location, and in a few cases, bottom topography. The occurrence of a species at a particular point was taken to mean one of several things: if the species was abundant, present in all stages and producing eggs, the conditions in that locality have been favourable in the recent past for the reproduction of that species; if the species was rare and represented by only a few stages, it was then considered in some instances to be scattered from a larger population. In the latter case, it was difficult to distinguish a population which was increasing from a group of individuals merely surviving. Each case, however, was treated separately and no overall interpretation was used. With these criteria it was possible to locate the areas in which several species were breeding as well as the dispersal of individuals from these areas.

A means for distinguishing individuals from different breeding areas was found in the variation in the length of the adult copepods. Ussing (1938) has found that the size of copepods varies with the locality. He attributes this to

the effect of temperature on the rate of development. In colder water a copepod would develop more slowly, spend a longer period eating and growing, and thus reach a greater size than a copepod developing in warmer water having the same food conditions. In any particular locality where a species had bred and developed, the variation in the size of the adults would be expected to be fairly small because the effect of temperature and food would influence all the individuals to the same extent. This was found to be the case for several species.

The interpretation of this phenomenon, however, is precarious. Ussing does not consider that in the lower temperature the rate of ingestion and assimilation would also be slower, so that the effect of temperature in lengthening the feeding period would be cancelled. It has been suggested that the size difference has a genetic basis. Yashnov (1955) reports that the larger copepods previously named *Calanus finmarchicus* in the Arctic belong to another species. The size variations encountered in the Queen Charlotte Islands Area, however, were in the order of one millimeter, hardly enough to warrant naming a new species. It is also possible that adults from different broods were measured. Digby (1950) found that where a species produced more than one brood a season, the size of the adults from the different broods varied. It has been found that *C. finmarchicus* reaches maturity in 28 days in the vicinity of the British Isles but this period is longer in more northern waters (Sverdrup, Johnson and Fleming, 1952). As the copepods in this study were collected within a period of 21 days it is not likely that adults from two broods were captured.

Whatever the cause of the size variation is, growth appears to be influenced by environmental conditions. The fact that there was small variation in the adult size in a local breeding population suggests that the effect of the environment was equal on all the individuals. As the size ranges of different populations were found to be different, it was assumed that, regardless of the lack of proof for the cause of the variation, its mere existence was useful in tracing the dispersal of individuals from their breeding areas.

In Dixon Entrance the size ranges of several species were determined in order to find the extent and direction of dispersal. These species were measured from the tip of the head to the end of the caudal furcae. Significant differences in the size ranges were apparent.

Marked differences in the proportions of the age classes of a few species were considered in one or two cases to indicate population distinctiveness. But only when the water mass in that locality was shown to be distinct by size differences in other species or by the presence of different species. This method was more effective in considering the dispersal of the subsurface species in which the age groups had a definite vertical distribution. The presence of only young indicated that they had drifted from over the deeper water in which the adults bred.

The term population refers in this study to a group of animals of one species which has developed in one area at one time. It is also used in this sense by Barnes and Marshall (1951).

SPECIES TAKEN

The water flowing past the Queen Charlotte Islands comes from the northern portion of the North Pacific Drift (Sverdrup *et al.*, 1952). This broad diffuse current divides just south of the islands. The northern portion, moving up the coast, has a fairly uniform temperature which fluctuates seasonally but rarely warms to above 10° C. With these temperature characteristics, the water in this area would be included in what Giesbrecht has termed "the northern cold water faunistic zone" (Giesbrecht, 1892; Ekman, 1953). As the division between the fuana of the northern cold water and that of the central warm water is stated to be approximately near the 15° C. isotherm, the area being studied was considered part of the northern cold-water zone although it is close to its southern limits.

Thirty-two species of copepods were identified, as listed below. An asterisk indicates an identification not completely certain.

SUB-ORDER CALANOIDEA

Acartia clausi Giesbrecht
A. longiremis (Lilljeborg)
Aetideus armatus (Boeck)
**Bradyidius similis* (Sars)
Calanus cristatus Krøyer
C. finmarchicus (Gunnerus)
C. tonsus Brady
Candacia columbiae Campbell. (North Pacific only)
Centropages mcmurrichi Willey
**Chiridius gracilis* Farran
Clausocalanus acuicornis (Dana)
Epilabidocera amphitrites (McMurrich). (North Pacific only)
Eucalanus bungii Giesbrecht
Euchaeta japonica Marukawa
Eurytemora hirundoides (Nordqvist)
Gaetanus sp.
**Heterorhabdus proximus* Davis
Metridia longa (Lubbock)
M. lucens Boeck
Paracalanus parvus (Claus)
Pleuromamma sp.
Pseudocalanus minutus (Krøyer)
**Rhincalanus nasutus* Giesbrecht—one specimen seen
Scolecithricella minor (Brady)
S. subdentata (Esterly)
Tortanus discaudatus (Thompson and Scott)

SUB-ORDER CYCLOPOIDEA

Corycaeus affinis McMurrich. (North Pacific only)
Oithona helgolandica Claus
O. plumifera Baird
Oncaea conifera Giesbrecht

SUB-ORDER HARPACTICOIDEA

Microsetella norvegica (Boeck)
M. rosea Dana

These species are northern cold water forms, although a few are also found in warm water. Three are peculiar to the North Pacific. The distribution of the commoner species at the stations can be seen in Table A of the Appendix, while collections of scarce species are shown in Table B.

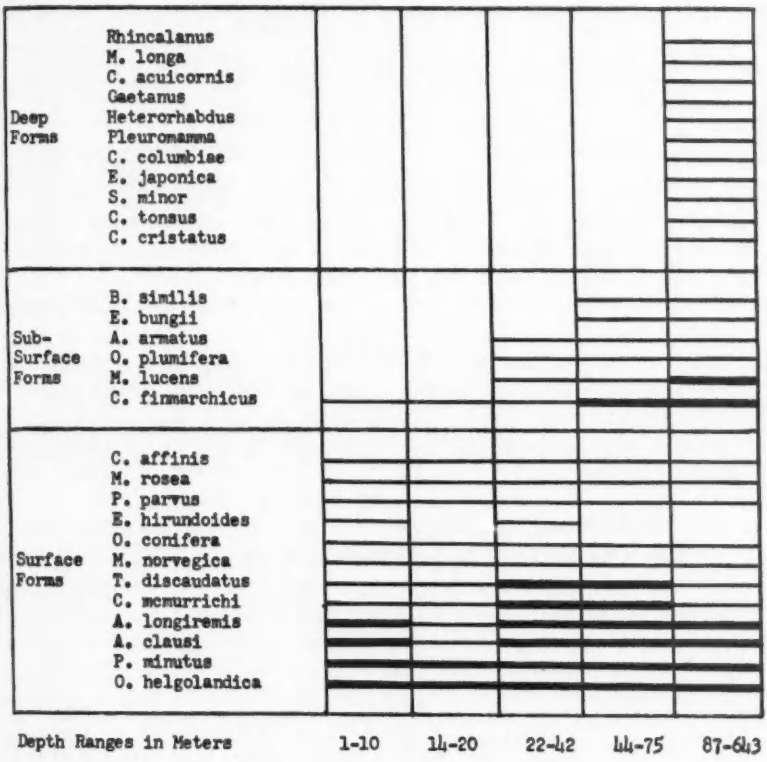

FIG. 2. The occurrence of copepod species in samples taken from different depths to the surface.

The vertical distribution of these species is shown in Figure 2. The stations have been grouped according to depth. If a species was present in the samples taken from a particular depth group, its occurrence was indicated by a line. A heavy line illustrates that a species was found in more than 50 percent of the samples in that particular group and a light line means that it occurred in less than 50 percent. Although *Calanus finmarchicus* was caught in a few cases near the surface, because it was more common in the deeper water it was considered as a subsurface form. Of the species which were caught in hauls of 22 meters or more, *Bradyidius similis* is benthic and will be not considered as part of the plankton. *Aetidius armatus* and *Epilabidocera amphitrites* were too scarce for further consideration.

The upper limits to the vertical distribution of the sub-surface species could be roughly determined by comparisons of adjacent stations, in which one of the species was either absent or rare. The compared stations are shown in Table I.

TABLE I. Stations compared in determining the upper vertical limits of three species.

Calanus finmarchicus				*Metridia lucens*				*Eucalanus bungii*			
Present		Absent		Present		Absent		Present		Absent	
Sta. No.	Depth *m.*	Sta. No.	Depth *m.*	Sta. No.	Depth *m.*	Sta. No.	Depth *m.*	Sta. No.	Depth *m.*	Sta. No.	Depth *m.*
64	44	68	23	97	65	90	36	81	135	90	36
104	75	103	36	83	366	86	91	83	366	86	91
99	91	72	33	...	...	...	...	114	164	108	100
97	65	90	36	119	173	122	104	82	206	96	46
86	91	85	55	110	33	109	24	...	...	...	...
111	119	108	100	...	...	...	...	...	...	...	...
112	91	113	45	...	...	...	...	...	...	...	...

The depths of the shallow stations were considered to be the depths of the upper limits of the species distribution. These are seen to be quite variable. This variability prevents the detailed use of average depth distributions for any one area. Instead, local upper limits have been used for particular areas except in one case (page 186).

TABLE II. Size ranges in millimeters of several species of copepods found in Dixon Entrance.

Sta.	*A. clausi*	*A. longiremis*	*T. discaudatus*	*C. mcmurrichi*
		ADULT MALES		
99	...	0.95–1.01	1.53–1.80	1.43[a]
98	0.70–1.00	...	...	...
97	...	...	1.73[a]	1.41
71	...	1.00–1.06	...	...
73	...	...	1.86–2.10[b]	1.27–1.60
75	...	...	...	1.30–1.44
96	0.72–0.75	0.96–1.01	1.52–1.77	1.44–1.78
88	...	0.90[a]	...	...
90	0.72–0.78	0.90[a]	...	1.25–1.33
91	0.91–1.00	0.92–1.00	1.36–1.50	1.24–1.55
		ADULT FEMALES		
99	...	1.17–1.31	1.87–1.94[b]	...
98	0.85–1.04	...	1.62[a]	...
71	...	1.20–1.40	...	...
73	0.92–0.97	...	...	1.48–1.52
75	...	...	1.70[a]	...
96	0.90–0.93	1.14–1.35	1.63–2.40	1.52–1.83
88	...	1.20–1.25	...	...
90	0.88–1.00	1.15–1.25	...	1.45–1.69[b]
91	0.95–1.12	1.07–1.27	1.35–1.57	1.40–1.72

[a]1 specimen measured.
[b]2 specimens measured.

Finally, eleven species were caught only in the very deep water, 87 meters or more. These are the species listed in Table B (Appendix), excepting *Eurytemora* and *Bradyidius*. Their stations are mostly off the shelf on the west coast and in the deeper regions of Dixon Entrance. These species were not represented by great numbers and were not widespread. Half of them were caught in only two or three of the very deep hauls. They are presumably characteristic of the deep oceanic water.

Measurements of several species in Dixon Entrance are recorded in Table II.

DISTRIBUTION OF THE MORE COMMON SPECIES

The horizontal distributions of some of the more common species were considered in detail. Each was studied separately because each as a species has its own physiological limits, seasonal fluctuations and vertical distribution.

Species Living near the Surface

Paracalanus parvus

P. parvus was found in the upper 14 meters of water in seven out of nine stations where supplementary hauls were taken (Table A, Appendix). At five of these stations the numbers caught in the deep haul approximated those in the shallow hauls, so it was assumed that *P. parvus* was living almost entirely at the surface. At two stations it occurred below 14 meters as well as at the surface. At the remaining two stations it was rare and was caught entirely below the surface. The species was therefore considered as a surface form rarely occurring below 14 meters.

P. parvus was common at three localities (Fig 3). In Dixon Entrance there was no indication that the species was breeding there or that it had drifted in from outside the sampled area. In Thetis and Tasu Inlets it was also common but absent in the water immediately outside the inlets. It seems likely that this species had increased locally in both areas.

It is possible that the very high surface temperatures recorded from these inlets may have had an influence on the abundance of the species. Giesbrecht (1892) states that although this species is characteristic of all three faunistic zones, its northern limit is the 10° isotherm. As a winter temperature of 7.7° was recorded by Barber and Tabata (1954) in the surface water of Dixon Entrance, it is quite possible that *P. parvus* occurs in the Queen Charlotte Islands area very close to its northern limit. If this is the case, then temperature as a limiting factor would be expected to influence its occurrence as well as its abundance.

Acartia clausi

A. clausi occurred immediately below the surface in most areas and did not appear to extend much deeper than about 15 or 20 meters. Only at two stations was it found completely below 14 meters.

FIG. 3. The distribution of *Paracalanus parvus*.

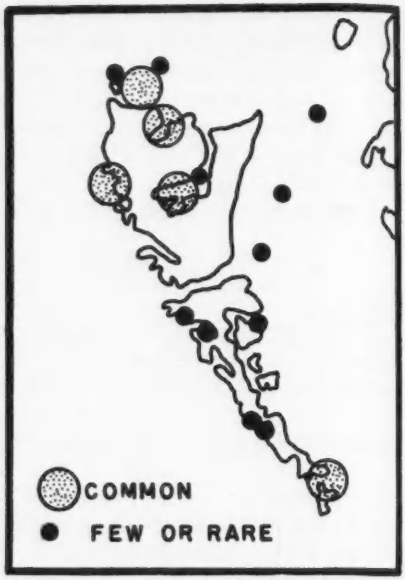

FIG. 4. The distribution of *Acartia clausi*.

The species was most common in three localities (Fig. 4). The greatest numbers were found in Dixon Entrance and Naden Inlet. For some reason it was absent from the surface water of the deeper stations. As this species is euryhaline, it may have preferred the low salinity water found at the surface near land where runoff supplies fresh water.

Temperature, however, may also have an influence on the seasonal fluctuations in the numbers of these copepods, Giesbrecht (1892) has noted that *A. clausi* is characteristic of the warm and northern cold water but it is limited to the north by the 11° isotherm. Its profusion in the localities mentioned may be due to the previous as well as present existence of low salinity warm water.

In addition to the above factors, the effect of scattering from local populations was evident in Dixon Entrance. *A. clausi* was studied here in more detail. By determining the size ranges of the animals at different stations, it was possible to distinguish two separate populations and their distributions. The results may be seen in Figure 5.

The distinct separation between the size ranges of the copepods at stations 96 and 91 is striking. At station 90, the males belonged with the population at station 96, while the females were a mixture of animals from stations 96 and 91. Station 98 contained a mixture of copepods of both sexes from stations 96 and 91. The mixing and spreading of these populations suggested the currents (Fig. 5) which may have been responsible. These will be discussed later in the account of Dixon Entrance as a whole.

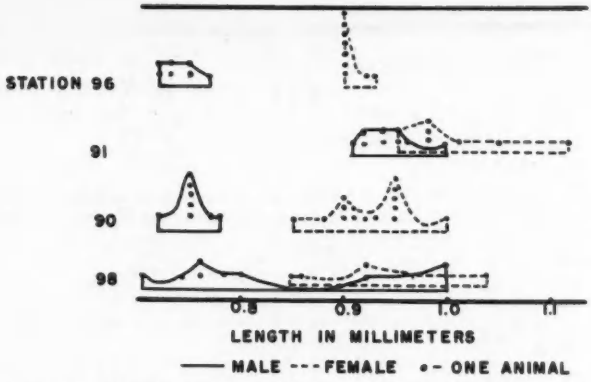

FIG. 5(a). The size variation of *Acartia clausi* in Dixon Entrance.

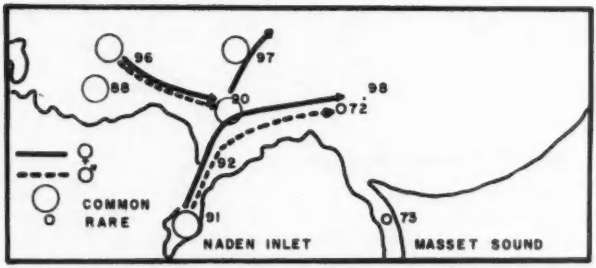

FIG. 5(b). Currents suggested by this variation.

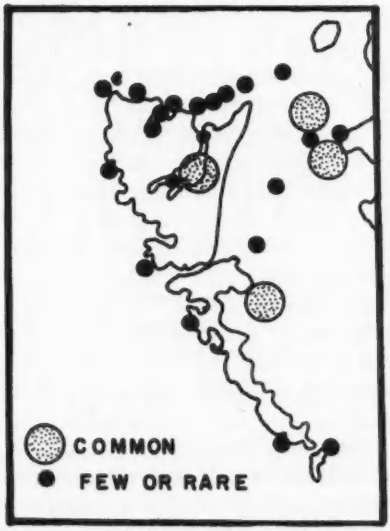

FIG. 6. The distribution of *Centropages mcmurrichi.*

Centropages mcmurrichi

C. mcmurrichi was found at 26 stations most of which were in Dixon Entrance and Hecate Strait (Fig. 6). Twenty of these had supplementary hauls, the results of which gave a fairly good indication of the vertical distribution. Table III summarizes the results.

TABLE III. The vertical distribution of *Centropages mcmurrichi* as indicated by its occurrence in supplementary ("shallow") and deep hauls. (C—common; F—few; R—rare; an asterisk indicates immature specimens only.)

Station No.	Shallow Depth *m.*	Shallow No.	Deep Depth *m.*	Deep No.	Time
131	14	R*	...	...	19.30
68	1	R*	...	C	20.15
70	1	R*	...	...	01.45
72	...	...	3	R	06.42
73	3	R	...	C	08.00
126	...	...	14	R	08.00
64	1	R*	...	C	08.10
71	...	...	1	F	09.00
69	1	R	...	...	10.55
127	...	...	14	R	11.30
85	...	...	3	R	13.13
119	...	...	14	R	13.30
86	...	...	3	R	13.50
114	...	...	14	R	14.00
128	16	F*	...	...	14.15
87	...	...	3	R	15.00
121	...	...	16	F*	16.30
AR	...	...	16	F	16.30
88	3	R	...	...	17.15
130	...	...	16	R	17.30

Although there were few hauls made at night, at these, *C. mcmurrichi*, especially the young stages, was found up to the surface. During the day there was some tendency to remain below. At the time when it was at the surface, it was represented by the whole of a small population or by the upward extension of a large population. It would seem that *C. mcmurrichi* lived just below the surface with the younger stages uppermost. Although at times it occurred above 14 meters, it showed a tendency to move down during the daytime. Most of the copepods, however, lived slightly below 14 meters.

C. mcmurrichi was most common in Hecate Strait. In Dixon Entrance it was common only at one station, while on the west coast it was rare and scattered, represented by a few immature specimens. This situation suggested that seasonal fluctuations were responsible for the difference in numbers. The small separate populations on the west coast and in Naden Inlet appeared to be populations increasing under the present conditions. The data, however, did not indicate anything definite.

Scattering by currents did appear to be responsible for some rare occurrences in Dixon Entrance. It has been indicated that *C. mcmurrichi* lived slightly below the surface, extending into deeper water than that occupied by *A. clausi*, and thus was subject to different water movements. *C. mcmurrichi* was common

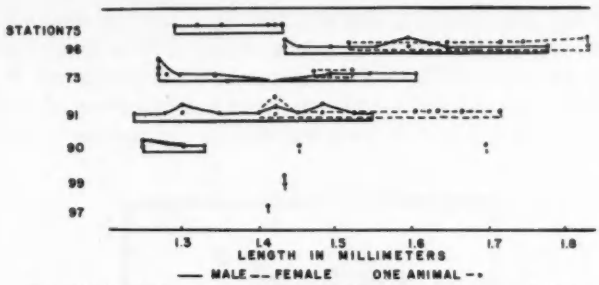

FIG. 7(a). The size variation of *Centropages mcmurrichi* in Dixon Entrance.

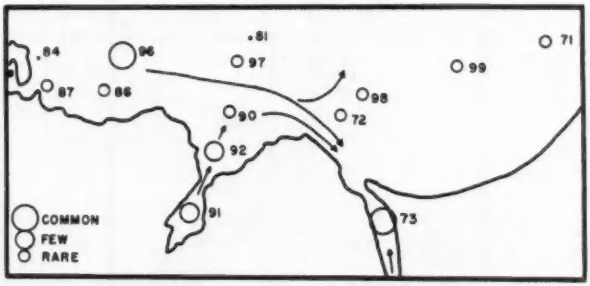

FIG. 7(b). Currents suggested by this variation.

at three localities, station 96, Masset Sound and Masset Inlet (Fig. 7, 24). There is no indication that individuals from station 96 were moving westward through station 91. However, the large individuals in Masset Sound could only have come from near station 96. The smaller copepods at station 73 could have come from the entrance to Naden Inlet or from inside Masset Inlet or from both. The size range of the copepods in Masset Sound suggests that water movements had transported some specimens into the sound from the west and possibly from Naden Inlet. Some of these could have come also from Masset Inlet. The westward current slightly below the surface in Dixon Entrance at the time of sampling, however, was not too distinct.

The eastern part of Dixon Entrance contained very few specimens of *C. mcmurrichi,* too few for measurements. Because of the predominance of young stages here, it does no seem likely that they have come from the west.

Tortanus discaudatus

The vertical distribution of this species was deduced from the results of 25 stations which had supplementary hauls. At most of these stations *T. discaudatus* did not occur above 14 meters. At 6 stations it was present above as well as below. The eggs occurred both above and below 14 meters.

Johnson (1934a) has indicated that this species is very widespread although

rarely becoming abundant. Its profusion in the sampled area could not be related to the physical characteristics of the water at 20 meters. As this species even in its young stages feeds on animals such as small protozoans, it is possible that its abundance was related to the quantity of a great variety of other plankton animals. As these food conditions were not studied, the reasons for its abundance are lacking.

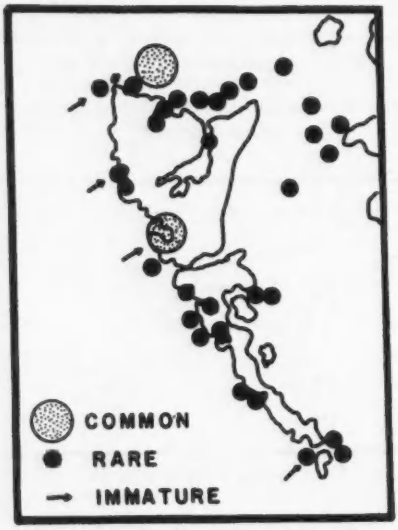

FIG. 8. The distribution of *Tortanus discaudatus*.

The species, however, was very widespread (Fig. 8) a result perhaps of its vertical distribution. Its occurrence mostly below 14 meters might have enabled the adults to remain inside the inlets with shallow sills, as well as in the slower moving sub-surface waters outside the inlets. On the other hand its occasional presence in the surface water would have brought it under the influence of faster currents. The water below 14 meters, however, must have been responsible for the distribution of this species.

This dispersal was evident in Dixon Entrance where *T. discaudatus* was measured. The results of this analysis are seen in Figure 9. Although scarce in Dixon Entrance, it was distinctly larger here than in Naden Inlet. Because the size ranges of copepods measured from different stations in Dixon Entrance were so similar, it was assumed that only one continuous population was present there. There was only a slight suggestion in the size of a female at station 92 that a few Naden Inlet copepods were spreading out into the open water. One of the two copepods measured in Masset Sound was, however, unusually large. This individual probably did not come from inside Masset Inlet because there *T. discaudatus* was extremely rare. Besides, the one specimen that was measured in Masset Inlet was much smaller than those in the Sound. The other copepods

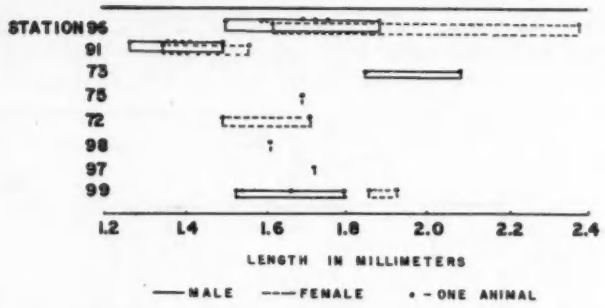

FIG. 9(a). The size variation of *Tortanus discaudatus* in Dixon Entrance.

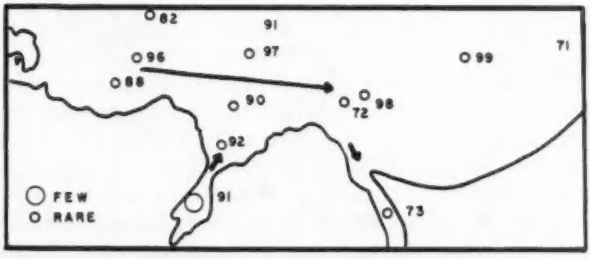

FIG. 9(b). Currents suggested by this variation.

measured from the sound fell within the size range of the Dixon Entrance copepods. It could have originated from station 96 or less likely from station 99. As the size variation of *C. mcmurrichi* also indicated a sub-surface inflow of Dixon Entrance water into Masset Sound, it is quite possible that this is also suggested by the distribution of *T. discaudatus*.

Oncaea conifera

The vertical distribution of *O. conifera* was made fairly clear from the results of extensive sampling at station 89 in Masset Inlet. The samples here were taken from water pumped from discrete depths. This method made the analysis easier and more accurate.

At station 89 it was evident that this species inhabited water from a depth of 75 meters to the surface. The eggs, however, were present only at 50 or 60 meters. This situation suggested that breeding occurred in the deeper water. In Tasu Inlet *O. conifera* occurred in the sub-surface as well as in the surface water. The eggs here were present in hauls taken from 14 meters. From the temperature data from both localities (Fig. 10) it is evident that the eggs were being laid at a temperature of about 11°C.

All the stations where *O. conifera* occurred had temperature allowing breeding. In Figure 10 the temperature curves are shown for stations where *O. conifera*

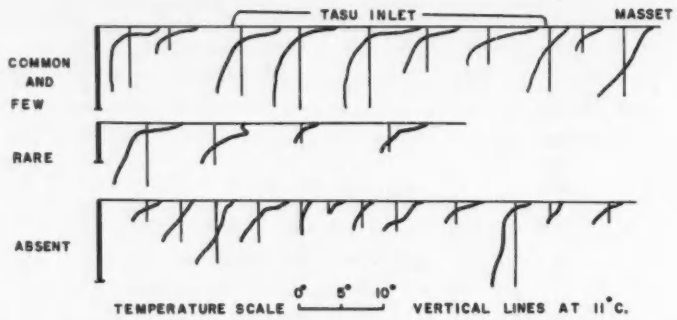

FIG. 10. The relationship of temperature to the distribution of *Oncaea conifera*.

was (a) common or few; (b) rare; (c) absent. The last group was made up of stations in the west coast inlets. These were chosen on the grounds that *O. conifera* seemed to typify inshore waters (Fig. 11). The stations where *O. conifera* was present were all characterized by a high surface temperature, above 13.5° C. Of the stations where *O. conifera* was absent but having temperature at which it could breed (127, 128, 129, 105, 108, 109 110, 117) only three had high surface temperatures and those (109, 110, 117) were shallow with very little water below 11° C. It would seem then that *O. conifera* became common in localities where there was a fairly deep layer of water below 11° as well as warm surface water. Perhaps the development of the young requires a high temperature. This apparent dependency on the warm surface water was sufficient to limit *O. conifera* to the inlets in this area. Nowhere in the outside water did the temperature rise above 13.5°.

O. conifera was represented by a few nonbreeding individuals at other stations (Fig. 11). On the west coast, four of these stations where eggs or both eggs and adults were absent are seen to be slightly north of the main population centers of Tasu and Thetis Inlets. The distribution suggested scattering by a a northward moving current in this area. From Tasu Inlet, *O. conifera* was presumably swept out in the surface water and carried northward. Only a nonbreeding part of the population moved out here as no egg sacs were found at station 124. Its rarity farther north may indicate that it was dying or was being widely dispersed. In three inlets to the north, however, *O. conifera* was represented by a few individuals in the deeper water below 14 meters. If the circulation of the water in these inlets was typical, then the surface water was moving out and was being replaced by inwardly flowing deeper water. The unusual occurrence of *O. conifera* in the deep water perhaps suggests that at the time of sampling it was being carried into these inlets in the deeper water from the outside.

Scattered individuals also occurred in Dixon Entrance. As these could not have drifted out of Masset Inlet or Naden Inlet, it would seem likely that they came from north of the sampled area.

Corycaeus affinis

C. affinis was distributed much like *O. conifera*. Breeding populations were present in Tasu and Thetis Inlets (Fig. 12), although they were not so obviously

FIG. 11. The distribution of *Oncaea conifera*.

FIG. 12. The distribution of *Corycaeus affinis*.

breeding as was *O. conifera*. The relatively large number of this species in Thetis Inlet was assumed to have arisen there. In Tasu Inlet a female carrying an egg sac was seen. The rarity of egg sacs may mean merely that the copepods were just beginning to mate. *C. affinis* was more common in Puget Sound where many females carrying egg sacs have been noted.

It is difficult to say that *C. affinis* breeds in the same conditions as does *O. conifera*. It was, however, common where the warmest surface water of the area was found. This may be significant to the development of the young although the species was not always found in the surface layer.

There were some apparently scattered individuals of *C. affinis* at five other stations. The locations of these, however, give no clue to the origin of the individuals. They may have come from outside the sampled area.

SUB-SURFACE SPECIES

The three species *Calanus finmarchicus*, *Metridia lucens* and *Eucalanus bungii* were limited to the deeper water (Fig. 2; Table A of the Appendix). The vertical distribution of the age groups of the first two species was determined from the data of station 89 in Masset Inlet (Fig. 26; Table C of the Appendix). The young of both species occurred closer to the surface than did the adults. Both sexes of *M. lucens* lived at approximately the same depth. The male *C. finmarchi-*

cus, however, appeared to occur in deeper water than did the female. The absolute depths are not considered typical, as *M. lucens* adults were certainly limited to water deeper than 30 meters in Dixon Entrance. Because of the scarcity of *E. bungii,* it was not possible to determine the distribution of the age groups.

The data from station 89 also indicated that *C. finmarchicus* and *M. lucens* performed a diurnal vertical migration. Both species showed some tendency to move up from the deeper water at night (Fig. 23). Other authors (Clark, 1933; Nicholls, 1933) have found the same behaviour in these two species. According to Esterly (1911b), *Eucalanus elongatus,* a close relative of *E. bungii,* does not migrate vertically in San Diego Bay. Whether or not this is typical also of *E. bungii* in the Queen Charlotte Islands area is not known. This species, however, was not found in the more shallow hauls which captured *C. finmarchicus* and *M. lucens.*

Calanus finmarchicus

The horizontal distribution of this species can be seen in Figure 13. The restriction of the adults to the deeper water is very noticeable, as well as the wider distribution of the younger stages. Although it could not be shown that the young lived permanently in the more shallow water of Dixon Entrance, it is quite possible that during their vertical migration they came up into the surface water long enough to be transported onto the shallow areas. This effect was also noticeable in Tasu Inlet, where the young moved into the shallow arms away from the main population of adults in the deep part of the inlet. In both these localities scattering was probably the result of a current just above 50 meters.

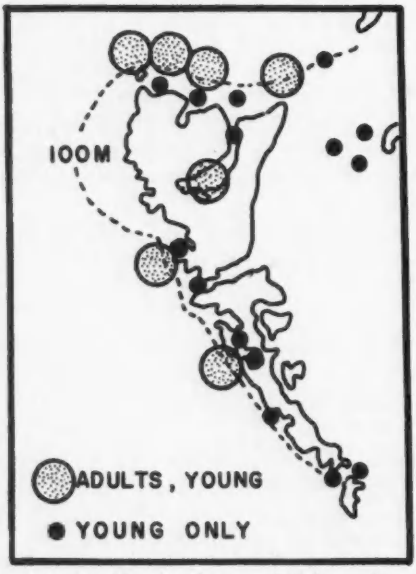

FIG. 13. The distribution of *Calanus finmarchicus.*

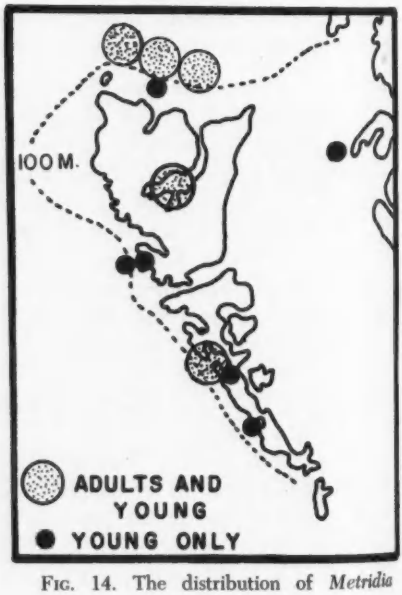

FIG. 14. The distribution of *Metridia lucens.*

Metridia lucens

The distribution of *M. lucens* suggested that it was limited to deeper water than was *C. finmarchicus* (Fig. 14). The upper limits to its vertical range in different areas (Table I) also indicates this. Its restriction to the deeper water is probably responsible for the lack of dispersal of the young stages. In only two localities, off Naden Inlet and in Tasu Inlet, was this effect evident.

Eucalanus bungii

As this species was so rare, no conclusions could be drawn from the age distributions. Stage V copepods and adult females were present in nearly all the samples in which the species was found.

The upper limits to its vertical distribution were very similar to those of *M. lucens*. In spite of this, *E. bungii* did not spread onto the shallow areas (Fig. 15) as did the other two species. It is quite possible that if *E. bungii* did not perform a diurnal vertical migration, its absence in the more shallow water explains its lack of dispersal onto the shelf.

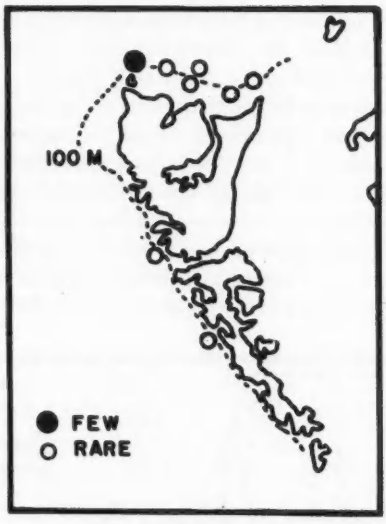

FIG. 15. The distribution of *Eucalanus bungii*.

CURRENTS SUGGESTED BY THE DISPERSAL OF COPEPODS

The distribution of all the species including those which were rare are now considered in several areas with suggestions of possible current patterns.

TASU INLET

Tasu Inlet is a fairly large and highly productive body of water on the west coast of Moresby Island (Fig. 1). At the time of sampling its plankton consisted

largely of copepods. The composition of the fuana, however, reflected the influence of the open ocean by the presence of salps and siphonophores, as well as water from the shallow areas characterized by pelecypod larvae. The results of 7 deep plankton hauls along with considerations of the physical data and topography give some idea of its circulation.

Tasu Inlet consists of three long bays. These are fairly shallow, about 30 or 40 meters. Wright Inlet (Fig. 17) has a deeper section (175 meters) but the depth in this inlet lessens to the north to about 50 meters. The central part of Tasu Inlet is mostly deeper than 100 meters. A shallow sill of about 30 meters, however, separates this deep section from the open ocean.

The surface temperatures were high, up to 19° C. in Botany Bay. These high temperatures were also present in the main part of the inlet but not immediately outside the sound. The temperature decreased sharply with depth, water at 20 meters being about 10°. The deeper water at station 118 was near 7°. The salinity also increased sharply with depth from about 28‰ at the surface to 32‰ at 20 meters. In the deeper water at station 118 it was as high as 33‰.

The distribution of surface plankton, although it was scarce, did suggest some outward flow of surface water. Two rather restricted species common in Tasu Inlet, *Oncaea conifera* and *Paracalanus parvus* were found in almost all the surface samples, although the majority occurred below 14 meters. Only two other species, *Oithona helgolandica* and *Pseudocalanus minutus* were also consistently found at the surface, but as these were so widespread it was not possible to determine the centers of population increase. *O. conifera* and *P. parvus* seemed to breed in the three bays (Fig. 16). They occurred in lesser numbers, *O. conifera* without its egg sacs, at station 118. Only *O. conifera* reached station 124, presumably via a surface current. As the temperature was low and the salinity high here, considerable mixing must have occurred between stations 118 and 124. The presence of *O. conifera* suggests that some of the mixed water must have originated from the surface of station 118. A surface outflow from Wright Inlet

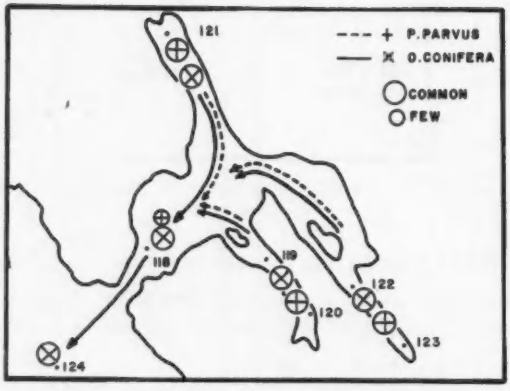

FIG. 16. A proposed circulation of the surface water above 14 meters in Tasu Inlet.

and Botany Bay was also suggested by the distribution of *Corycaeus affinis* represented there by a few individuals (Fig. 17).

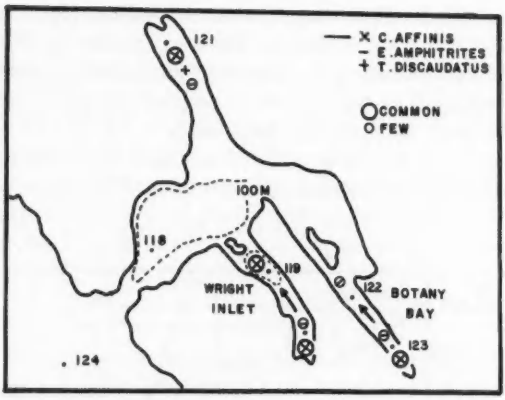

FIG. 17. A proposed circulation of water between about 14 and 30 meters in Tasu Inlet.

Species occurring below 14 meters as well as in the shallow water were apparently limited to the bays (Fig. 17). Although these copepods were represented by few individuals, their lack of dispersal suggested that water between 14 and 30 meters was not moving out of the bays. Also, the abundance of *Oncaea conifera* and *Paracalanus parvus* which occurred mostly below 14 meters implies that very little water at these depths was moving out.

The bottom water of the bays may be typified by the presence of *Calanus finmarchicus*. In Figure 18, the distribution of the adult and late copepodid stages

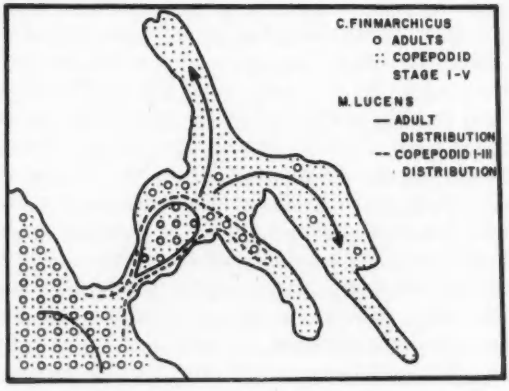

FIG. 18. A proposed circulation of the deep water of Tasu Inlet.

is seen to be in the deeper water only. The young, however, living above the adults appear to have spread onto the shallow bays indicating an inward flow of water just above 50 meters and possibly up to 25 meters. *Metridia lucens* seemed to be restricted to the deeper water at station 118. The presence of a few young individuals at the station in the deep pocket in Wright Inlet, however, suggests that strays had been carried over the sill into the inlet at about 50 meters. The remaining species in the deep part did not seem to scatter. This suggests very little movement of the deep water.

The relationship of the deep water inside the sill to that outside is illustrated by a comparison of stations 118 and 124 (Fig. 19). Five species lived

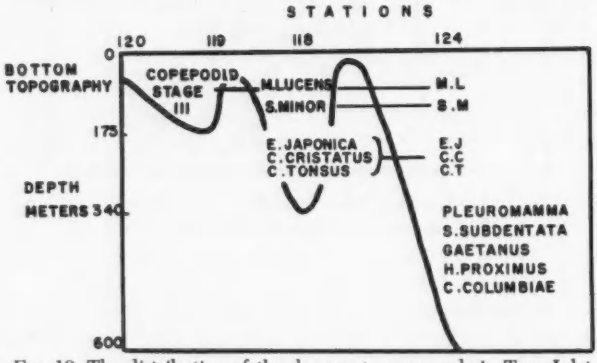

FIG. 19. The distribution of the deep water copepods in Tasu Inlet and immediately outside.

inside below 100 meters, *Metridia lucens* and *Scolecithricella minor* being uppermost. Except for *M. lucens* all were represented by fewer individuals here than outside. At station 124 there occurred an additional five species presumably belonging to the deeper water. The presence of stage V copepodids and female adults of *Eucalanus bungii* is of considerable importance. By a comparison of adjacent stations in other parts, the upper limits of its vertical distribution was found to be near 36 to 100 meters. The upper limit of this species would then be about 6 to 70 meters below the sill depth. As *E. bungii* did not occur inside the inlet, it may be said that the water just below sill depth was not entering the inlet at the time of sampling nor did it do so in the time just previous to sampling.

Further evidence for the isolating effect of the sill may be seen in the population structure of *E. japonica*. The rare individuals at station 118 were all stage V copepodids. Outside the inlet, stages IV, V as well as an adult female and eggs were found. According to Campbell (1934), *E. japonica* breeds in the deep water between 200 and 400 meters. Here also the young develop. As *E. japonica* also occurred in the deep water in the Queen Charlotte area, in samples taken from 87 meters and deeper, it does not seem likely that at the time of sampling only stage V copepodids were being carried over the sill from the outside where other stages including eggs were found. At some time in the past when the

population outside perhaps consisted of only one stage (as is possible in the early spring), water from beneath sill depth may have carried a few individuals over the sill to the inner part of the inlet. At the time of sampling, however, it does not seem likely that water much below sill depth was moving into the inlet.

In this analysis it is suggested that a slow surface current was moving out of the arms into the main part of the inlet, some of it flowing over the sill. To balance this outflow, an inflow should have been present but it could not have been much deeper than about 36 meters. This depth was approximately the most shallow water in which *E. bungii* was found (Table I). This inflow could have been slightly deeper. The deep water in the center of the inlet was not mixing vertically and at the time of sampling was distinct from the deep water outside the inlet.

Dixon Entrance

The water immediately north of Graham Island was sufficiently well sampled to be investigated in detail. The presence of large areas of unsampled water to the north, however, made this analysis very difficult. The currents proposed are, thus, only suggestions but they do illustrate the possibilities for a use of plankton animal distribution.

Dixon Entrance has a narrow shallow shelf (Fig. 22). About 20 miles from the shore off Naden Inlet the depth increases to about 300 meters. Only one sample was taken from water of this depth, about five miles north of Langara Island. The water was cold, about 11° to 13°C. at the surface, to about 6° near the bottom at the deeper stations. The salinity ranged from about 30‰ to 33‰ at the surface. The deep water had a fairly uniform salinity of about 33‰.

The currents as estimated from the distribution of copepods will be considered in three groups; surface to about 10 or 15 meters (Fig. 20), between 15 and 30 meters (Fig. 21), and below 30 meters (Fig. 22).

The surface currents were suggested by the distribution of *Acartia clausi*, *Paracalanus parvus* and *Microsetella norvegica* (Fig. 20). The size variation of *A. clausi* was the best indicator of an eastward movement. Its scarcity in the east suggests that it was also being carried northward. The flow of surface water from Naden Inlet, as was indicated by the distribution of *A. clausi*, was also suggested by the distribution of *M. norvegica*. This species also occurred offshore from Naden Inlet and may possibly indicate an onshore current here.

An eastward movement of water at 15 to 30 meters was also evident in the size variations of *Centropages mcmurrichi* and *Tartanus discaudatus* (Fig. 21), the length of these copepods being comparable right aross the coast. Some flow of water out of Naden Inlet was also indicated but this seemed to be much less than the outward flow of surface water. Because these species were so scarce it was impossible to judge whether or not they moved north. There seemed to be, however, a separate water mass just east of stations 98 and 72. This was presumed from the presence of relatively large specimens of *A. longiremis* and from the age distribution of *C. mcmurrichi*. The latter species was represented by young

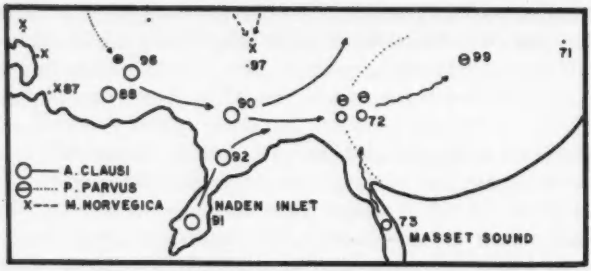

FIG. 20. A proposed circulation of the surface water in Dixon Entrance.

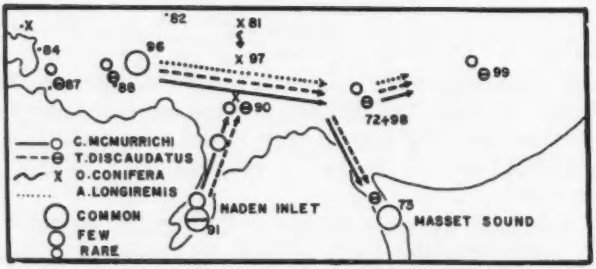

FIG. 21. A proposed circulation of water between 15 and 30 meters in Dixon Entrance.

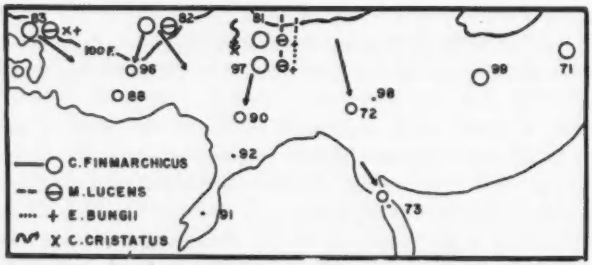

FIG. 22. A proposed circulation of water between about 40 and 100 meters in Dixon Entrance.

stages only, while in the west all stages were present. If the water in the east was a somewhat separate mass, then at least part of the water which has been shown to be moving eastward must move north from stations 98 and 72. This is only a deduction, however, and was not indicated very well by the plankton distribution.

Nor did it seem that the water in the eastern part of Dixon Entrance was originating from Masset Inlet. *C. mcmurrichi* was very common inside Masset Inlet. If the water had moved out of the inlet and towards the east, *C. mcmurrichi*

would not have been as scarce as it was in this eastern section. On the contrary, the large size variation of *C. mcmurrichi* in Masset Sound implies that at least some have come from farther west (station 96), or from near the entrance to Naden Inlet and a few possibly from inside Masset Inlet. The inflow of slightly sub-surface water into Masset Sound was also indicated by *T. discaudatus*, a species extremely rare in Masset Inlet.

Movements of the deeper water can be seen from the dispersal of the different age groups of *Calanus finmarchicus* and *Metridia lucens* (Figs. 13, 14). Only the young stages of these two species occurred in the shallow areas of the shelf while all stages were found in the deeper water. This distribution was probably the result of a movement of young from above the adult population onto the shelf presumably by an onshore current (Fig. 22). The young of *M. lucens* moved onto the shelf in only one place but immature individuals of *C. finmarchicus* occurred over most of the shelf. The latter species seemed to occur in more shallow water than did *M. lucens* in this area. The onshore current would have to have been above 40 or even 20 meters to spread *C. finmarchicus* onto most of the shelf. Off Naden Inlet, however, a deeper current probably at about 50 meters could have been responsible for the spreading of *M. lucens*. Upwelling in this region was suggested by the appearance at station 81 of *Calanus cristatus*, a species otherwise occurring in much deeper water (station 83) from about 300 meters. This species did not occur at station 82 at a depth of 206 meters.

Of special note was the spread of very young *C. finmarchicus* into Masset Sound (copepodid stages II and III). The origin of these could only have been the deeper water as only stage V was found inside Masset Inlet. The presence of these very young stages here, along with specimens of *C. mcmurrichi* and *T. discaudatus*, confirms the idea that water just below the surface was moving into Masset Sound at the time of sampling.

Masset Inlet

Masset was the largest of the inlets studied (Fig. 1). It is about 20 miles long and 5 miles wide. The western part, situated close to the mountains, is the deepest—about 80 meters as sounded from station 78 (Fig. 24). Towards the eastern region the water shallows to 20 meters. The narrow Masset Sound, about 20 miles long and 20 meters deep, connects the inlet at its northern extremity to Dixon Entrance.

At the time of sampling the surface water of Masset Inlet was warmer than the surface water of Dixon Entrance. At the surface of the inlet it was about 14°C., while in the deeper water it reached 8°. The salinity at the surface was 22‰. It increased slightly with depth. The salinity at the bottom, however, was less than that at mid-depth. Perhaps the low temperature of the deep water made the density great enough for stability. Although there were many rivers entering the inlet from all directions, the Yakun River entering the southeastern corner from a large drainage area to the south was thought to be the main contributor of fresh water.

The inlet was surveyed on July 20. Both a deep haul and a supple-

mentary haul were taken at each station. Station 89, however, was occupied for 24 hours of July 24. A supplementary haul, pumped-hose samples and a deep haul were taken four times during that period.

Ten species of copepods were found in Masset Inlet:

Centropages mcmurrichi	*Pseudocalanus minutus*	*Oncaea conifera*
Tortanus discaudatus	*Acartia longiremis*	*Calanus finmarchicus*
Epilabidocera amphitrites	*Acartia clausi*	*Oithona helgolandica*
Metridia lucens		

O. helgolandica and *P. minutus* were common and widespread in the inlet. Only rare specimens of *E. amphitrites* and *T. discaudatus* were captured. The six remaining species were sufficiently numerous and varied in concentration to indicate the physical factors influencing distribution.

The vertical distribution of the six species at station 89 can be seen in Figure 23 and Table C (Appendix). This diagram shows the relative abundance

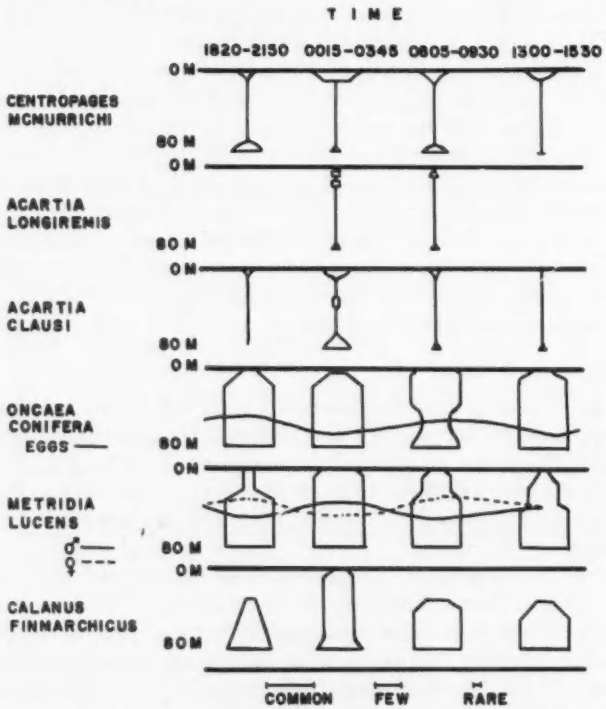

FIG. 23. The relative abundance and vertical distribution of copepods at station 89 in Masset Inlet over a 24-hour period.

of species at different depths over a 24-hour period. Three species, *C. mcmurrichi*, *A. longiremis* and *A. clausi* were living near the surface. *A. longiremis* seemed to

occur near 3 meters here. At other stations it occurred below this but it was assumed to be living just below 3 meters. *C. mcmurrichi* occurred from the surface to about 10 meters.

C. mcmurrichi was common and probably breeding in the upper 14 meters, as young were also found here. Its horizontal distribution and relative abundance are illustrated in Figure 24. The low salinity water, if Masset Inlet were typical

FIG. 24. The relative abundance and horizontal distribution of *Centropages mcmurrichi* in Masset Inlet.

of most inlets, would have tended to move out through the sound. *C. mcmurrichi*, however, was living and reproducing in this layer. It could not have become common if the surface water were being rapidly replaced. Its abundance therefore suggests only a slow movement of the surface water and the possible existence of eddies in the inlet.

A. clausi, unlike the aforementioned species, lived entirely in the surface 3 meters, most commonly opposite the mouths of large bays (Fig. 25). As was

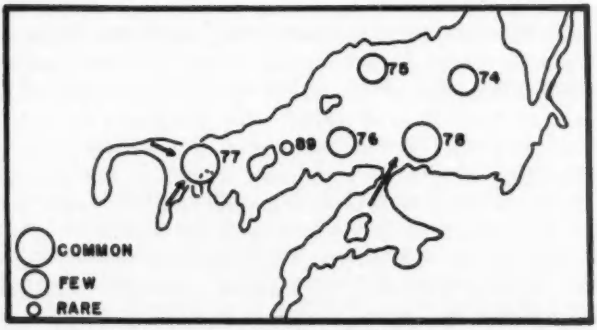

FIG. 25. The distribution of *Acartia clausi* in Masset Inlet.

seen in previous results, *A. clausi* was often common in bays typified by Naden Inlet. Also its vertical distribution made it subject to the outward flowing surface water. It is quite possible, then, that *A. clausi* was more common in the bays

opening into Masset Inlet. If so, these copepods could have moved into the main part and account for the large numbers at stations 77 and 78.

The three other species were most abundant in the deeper water, although they did occur near the surface. *O. conifera* and *M. lucens* occurred in fewer numbers near the surface but *C. finmarchicus* approached the surface only at night. The three species may indicate the movement of the deeper water.

Although *O. conifera* lived in the whole water column, females carrying egg sacs were seen in the pumped samples only from near 50 meters. Free egg sacs were also noted in the samples. As this species, characteristic of the superfamily Cyclopoidea, carries its egg sacs until they hatch, it can be assumed that the free egg sacs had fallen off the females after the sample was collected. The evidence suggests that *O. conifera* was reproducing in the deeper water at about 50 or 60 meters, and if so, it could only have been producing young in the western part of the inlet where these depths occurred. *O. conifera*, however, was found in lesser numbers and without egg sacs farther east (Fig. 26). Considering that production

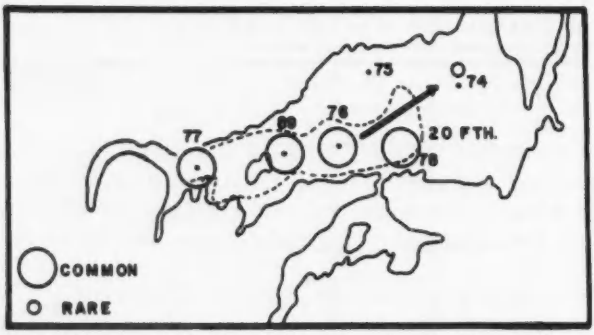

FIG. 26. The distribution of *Oncaea conifera* in Masset Inlet.

occurred only in the west, the individuals living above the depth where reproduction occurred must have drifted eastward away from their origin.

The vertical distribution of *M. lucens* was similar to that of *O. conifera*. The adults lived at about 30 to 50 meters, while the young occurred above this. The young were continually present, even if scarce, in the surface layer. Figure 27 (Table D, Appendix) indicates the population structure of this species at different stations. In Figure 28 the extents of the distribution of the adult and immature stages are indicated. Adults were present only in the western area, while stage V copepodids ranged farther east and stage I copepodids covered the whole area. As only the young were dispersed, the currents responsible for this must have been present above 30 meters.

C. finmarchicus was represented in Masset Inlet by copepodids of stage V, although a few adult females as well as a few stage IV copepodids were also seen. The species occurred entirely at stations 76, 77, 75, 89 (Table D, Appendix). Although it did move up to the surface at night, it was not dispersed as was

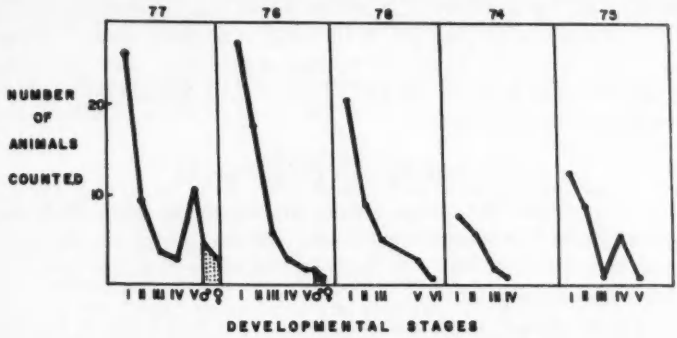

FIG. 27. The age structure of the *Metridia lucens* population in Masset Inlet.

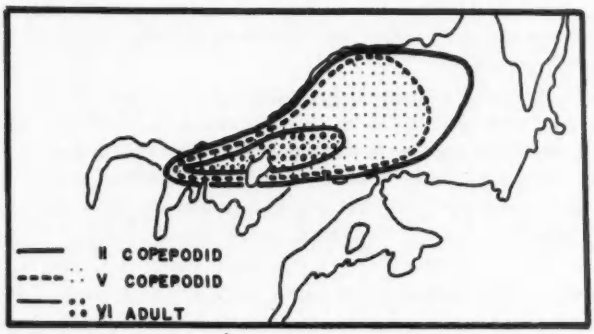

FIG. 28. The horizontal distribution of several immature stages of *Metridia lucens* in Masset Inlet.

M. lucens over the rest of the inlet. Hence, the current which spread the young of *M. lucens* must not have been very fast or steady as it did not cause *C. finmarchicus* to spread in the time that some of the population was near the surface.

The three species living in the deeper water appeared to be isolated in Masset Inlet by the long shallow sound. Two of them, *M. lucens* and *O. conifera*, were reproducing at the time of sampling but it is doubtful that *C. finmarchicus* was. It is very difficult to say whether the immature stages of *C. finmarchicus* present in the inlet were carried there or had been in the inlet for some time. It seems possible that very young stages of *C. finmarchicus* could have been carried into the inlet. At the time of sampling these stages were present in Masset Sound. It is not impossible that a strong inflow into the sound could bring a fair number of this species into the inlet.

In summary, it seems that there were no rapidly moving currents in Masset Inlet. As species living near the surface were able to reach large numbers by reproducing it is reasonable to suggest that very little surface water was moving

out over the sound at the time of sampling. There was some indication, however, that surface water was moving out of the bays. Also there seemed to be a slight eastward moving current above 30 meters. Apparently very little water was moving into the inlet over the sound as indicated by the absence of very young *C. finmarchicus* inside the inlet.

SUMMARY AND CONCLUSIONS

Thirty-two species of copepods were identified. All were characteristic of northern cold water. The vertical distribution of these species was also determined. The information obtained was very useful in the interpretation of factors influencing horizontal distribution.

Some species living in the surface water were presumed to be limited by temperature as they were only abundant in water with relatively high temperatures. It was also evident that several species living in the deeper water were dependent on the low temperatures there for breeding. In addition to temperature, low salinity seemed to correlate with the presence of one species, known to prefer water of low salinity.

Currents were also influential in scattering the copepods from the areas in which they were reproducing. These currents could be inferred from the direction of scattering of several species in three areas. In Tasu Inlet, the extent of surface outflow and sub-surface inflow were indicated. The deep water inside the sill was shown to be distinct from that outside. In Masset Inlet the surface outflow was not outstanding, instead, the existence of slowly moving eddies inside the inlet seemed evident. Species living in the deep water here also appeared to be isolated by the sound. Although no inflow from Dixon Entrance was evident at the time of sampling, it is suggested that periodically a fairly large amount of water must move into Masset Inlet from Dixon Entrance. A study of Dixon Entrance indicated an eastward flow of surface water as well as a movement of the deeper water onto the shelf particularly off Naden Inlet.

This study, although exploratory, has indicated some of the factors which need to be considered in future plankton studies. It has illustrated the biologist's need for knowledge of the physical conditions, especially the movements of water which have been shown to have a considerable effect on the distribution of copepods.

Also, many problems concerning the animals themselves have not been solved. A more basic knowledge of their seasonal fluctuations, vertical migrations and physiology is required for this area. It is felt that in order to solve these problems, plankton should be studied as such, and not as supplements to physical studies. As this study has shown, copepods have possibilities in current determinations but these will not be fully realized until more is known about the animals themselves.

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APPENDIX TABLES

TABLE A. Occurrence of 17 species of copepods in the collections studied. A—abundant; C—common; F—few; R—rare; e—eggs only; i—immature only.

Place	Station No.	Surface temp.	Depth of haul	*Oithona helgolandica*	*Pseudocalanus minutus*	*Acartia clausi*	*Acartia longiremis*	*Centropages mcmurrichi*	*Tortanus discaudatus*	*Microsetella norvegica*	*Oncaea conifera*	*Paracalanus parvus*	*Corycaeus affinis*	*Calanus finmarchicus*	*Metridia lucens*	*Epilabidocera amphitrites*	*Oithona plumifera*	*Artidens armatus*	*Eucalanus bungii*	*Scolecithricella minor*
		°C.	*m.*																	
Hecate Strait	68	14.8	23	C	C	...	F	C	C	...	...	R	...	R	...	...	...	...	...	...
			1	F	F	R	?	R	...	...	...	...	...	...	...	...	...	...	...	...
"	69	...	22	C	C	R	C	R	C	...	...	...	...	...	...	...	...	...	...	...
			1	F	F	F?	F	R	R	R	...	...	...	...	...	...	...	...	...	...
Cumshewa Inlet	64	14.5	44	F	A	F	F	C	R	...	...	...	...	R	...	...	...	...	...	...
			1	F	F	F	R	R	...	...	...	...	...	...	...	...	...	...	...	...
"	65	...	6	F	A	R	F	F	...	...	...	...	...	...	...	...	...	...	...	...
Hecate Strait	70		18	C	C	R	C	R	C	...	...	...	...	...	...	...	...	...	...	...
			1	F	F	R	F	R	...	...	...	...	...	...	...	...	...	...	...	...
"	103	11.8	36	F	C	...	C	C	F	...	...	...	...	Ri	Ri	Ri	...	...	...	...
"	104	...	75	R	C	...	C	F	R	...	...	...	...	C	...	...	...	...	...	...
"	102	...	69	C	C	...	C	R	R	R	...	...	R	Ci	...	...	...	...	...	...
"	101	...	27	C	C	F	C	C	...	...	...	F	...	...	...	...	...	...	...	F
Dixon Entrance	100	12.6	91	C	C	...	C	F	R	...	...	...	...	F	...	...	...	...	...	R
"	71	...	127	F	C	...	C	F	e	...	R	...	...	C	...	...	R	...	R	...
			1	Fi	...	...	Fi	...	...	...	...	...	...	...	...	...	...	...	...	...
"	99	12.7	91	R	C	R	C	R	R	...	...	F	...	C	...	...	R	...	R	R
"	98	...	47	C	F	F	C	Fi	R	...	...	R	R	...	...	...	...	...	...	...
"	72	12.0	54	C	C	R	A	R	R	...	...	R	...	R	...	R	R	...	...	...
			3	C	C	C	C	...	e	R	...	...	...	...	...	...	...	...	...	...

Masset Sound	73	...	15	C	C	C	C	C	R	...	...	...	...	...	...	...	...	...	...	...
			3	F	C	C	R	...	...	R	...	...	...	...	...	...	...	...	...	...
Naden Inlet	91	13.4	27	F	C	A	C	F	C	R	...	...	...	...	...	...	R	...	...	...
Virago Sound	92	11.9	8	F	R	C	F	F	Fi	F	...	...	...	...	...	...	...	...	...	...
"	90	11.9	35	C	F	C	R	R	R	...	R	...	...	R	R	R	...	...	...	...
Dixon Entrance	97	...	65	C	F	R	R	R	...	...	R	...	...	C	Ri	R	...	...	R	...
"	81	...	135	C	C	...	C	...	...	R	R	...	...	C	Ri	...	...	...	R	...
			10	C	C	...	A	...	...	R	...	...	...	...	...	...	...	...	...	...
"	88	...	42	C	C	C	C	R	Re	...	...	...	...	Ri	...	...	...	...	...	...
			3	C	F	C	...	R	...	F	...	...	...	...	...	...	...	...	...	...
"	96	...	45	A	C	C	A	C	Re	...	...	R	R	Ri	...	R	...	...	...	...
"	82	11.8	206	C	C	R	C	...	Fe	R	...	...	...	C	C	...	...	...	R	...
			10	C	C	C	C	...	...	...	...	...	...	...	...	...	...	...	...	...
"	83	...	364	C	C	F	F	...	e	F	F	...	...	C	...	...	...	...	F	R
			10	C	...	...	R	...	...	A	...	...	...	...	...	...	...	...	...	...
"	88	...	42	C	...	C	C	F	Fe	...	...	...	...	...	...	...	...	...	...	...
"	87	11.8	42	C	C	...	C	R	R	...	...	...	...	...	...	...	...	...	...	...
			3	C	...	F	F	...	...	F	...	...	...	...	...	...	...	...	...	...
"	84	...	10	C	F	C	C	...	...	F	...	...	...	...	...	...	...	...	...	...
			3	A	...	F	F	...	...	F	...	...	...	...	...	...	...	...	...	...
Pacific Ocean	86	...	91	C	C	...	C	R	...	...	R	...	...	Ri	...	...	...	...	...	...
			3	C	C	...	C	...	...	F	...	...	...	...	...	...	...	...	...	...
"	85	12.9	55	C	C	...	C	R	R	...	...	...	...	Ri	...	...	...	...	...	...
			3	C	...	...	C	...	...	F	...	...	...	Ri	...	...	...	...	...	...
Hussan Bay	LI	.	1	A	R	R	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Parry Passage	94	...	55	C	C	F	C	R	R	...	...	...	...	...	...	...	..	...	...	...
"	93	...	25	C	C	...	C	Ri	R	...	...	...	...	R	...	...	...	...	...	...
Dixon Entrance	99	...	22	C	C	R	R	R	R	...	...	...	...	R	...	...	R	...	...	...
Otard Bay	OB	...	14	C	...	R	...	...	Ri	...	...	...	...	...	...	...	...	...	...	...
Port Louis	106	...	26	C	C	C	...	...	Ri	...	...	R	...	...	...	...	...	...	...	...

TABLE A—(*continued*)

Place	Station No.	Surface temp.	Depth of haul	*Oithona helgolandica*	*Pseudocalanus minutus*	*Acartia clausi*	*Acartia longiremis*	*Centropages mcmurrichi*	*Tortanus discaudatus*	*Microsetella norvegica*	*Oncaea conifera*	*Paracalanus parvus*	*Corycaeus affinis*	*Calanus finmarchicus*	*Metridia lucens*	*Epilabidocera amphitrites*	*Oithona plumifera*	*Acartia hudsonica*	*Eucalanus bungii*	*Scolecithricella minor*
Kano Inlet	110	...	33	C	C	...	...	...	Ri	...	...	...	...	...	Ri	...	...	...	...	...
			14	C	C	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Kano Inlet (entrance)	108	12.7	100	F	C	...	F	...	...	...	...	...	...	R	...	...	...	...	...	...
Kano Inlet	109	...	24	R	Ri	...	...	...	Ri	...	...	...	...	...	...	...	...	...	...	...
Pacific Ocean	107	13.7	219	F	C	...	R	...	...	...	R	...	...	...	Fi	...	...	R	...	...
Van Inlet	111	...	119	C	C	...	F	...	R	R	R	...	...	C	...	...	R	R	...	...
			15	C	...	...	F	...	...	...	...	...	...	...	...	...	...	...	...	...
Pacific Ocean	114	14.8	164	C	C	...	R	R	R	...	...	...	...	R	...	...	F	...	R	...
			14	C	R	...	F	...	...	F	...	R	...	...	...	...	...	...	...	...
Dawson Harbour	113	15.1	45	C	C	...	...	...	F	...	R	...	...	...	...	...	...	...	...	...
			14	...	R	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Skidegate Channel	112	15.0	91	C	C	...	F	...	R	...	C	F	R	F	...	...	...	...	...	...
			14	R	...	...	...	?i	...	R	F	F	...	...	...	...	...	...	...	...
Security Cove	115	16.2	23	C	...	F	...	...	R	...	R	F	...	...	...	...	...	...	...	...
			14	a	...	...	...	...	...	F	...	...	...	...	...	...	...	...	...	...
Thetis Cove	116	17.6	24	C	...	F	...	...	F	...	F	C	C	...	...	F	...	...	...	...
			14	C	...	...	...	...	R	R	F	Fi	R	...	...	...	...	...	...	...
Louscoone Inlet	128	13.6	73	C	A	...	F	Ri	F	...	...	...	...	...	...	...	...	...	...	...
			14	C	F	F	...	F	F	F	...	...	...	...	...	...	...	...	...	...
Kootenay Inlet	117	15.0	48	F	A	...	R	...	F	...	...	...	...	...	...	...	...	...	...	...
			14	F	Ri	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...

Tasu Inlet	121	...	36	C	F	...	R	R	R	...	C	A	F	Fi	...	R	...	R	...	...
			14	R	...	...	...	...	...	...	C	C	...	...	...	...	...	...	...	...
'	123	18.3	30	R	R	...	...	...	...	...	C	C	F	F	...	R	...	R	...	...
			14	R	F	...	...	...	...	...	C	C	R	...	...	...	...	...	...	...
"	122	...	95	R	F	...	...	...	...	R	C	C	R	C	...	...	...	C	...	...
			14	F	...	...	R	...	...	R	C	C	R	...	...	...	...	...	...	...
"	119	18.7	175	F	F	...	R	R	...	...	C	C	R	C	R	...	...	F	...	R
			14	R	...	...	R	...	...	...	C	A	R	...	...	...	...	...	...	...
"	118	...	347	...	F	...	...	...	...	R	F	F	F	A	C	...	...	F	...	R
"	120	...	54	F	A	...	F	...	...	...	C	C	...	Fi	...	R	F	R	...	...
			14	F	C	...	...	...	...	...	C	C	F	F	...	...	...	...	...	...
Pacific Ocean	124	...	643	R	C	...	R	...	...	R	C	...	...	C	C	...	...	R	F	F
Gawgaia Bay	126	...	20	C	C	R	C	R	R	F	...	F	...	Ri	...	...	...	...	...	...
			14	C	...	F	...	...	...	R	R	...	R	...	...	...	...	...	...	...
"	125	15.8	36	C	...	R	C	...	Ri	...	R	...	...	...	Ri	Ri	R	...	...	...
Flamingo Harbour	127	...	50	C	C	...	F	R	C	...	...	...	...	...	...	...	...	...	...	...
			14	C	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Off Adam Rock	AR	...	120	C	C	...	F	F	F	...	...	...	...	...	...	...	F	...	...	...
			14	C	R	...	...	...	...	F	...	...	...	R	...	...	...	...	...	...
Louscoone Inlet	129	...	45	F	C	...	R	...	A	R	...	...	...	...	...	...	...	...	...	...
			14	F	F	...	F	...	C	R	...	...	...	Ri	...	...	...	...	...	...
Houston Stewart Channel	130	...	41	C	C	...	F	R	F	...	...	...	...	...	...	R	R	...	...	...
			14	C	F	...	R	...	...	F	...	...	...	...	...	...	...	...	...	...
Heater Harbour	131	13.4	20	C	...	C	C	Ri	Ri	...	...	F	R	...	...	...	...	...	...	...
			14	C	...	...	Ri	Ri	...	F	...	...	...	...	...	...	...	...	...	...
Masset Inlet	74	...	48	F	A	F	F	F	?	...	R	...	...	...	R	R	...	...	...	...
			3	C	C	F	...	F	...	...	...	...	...	...	R	...	...	...	...	...
"	75	...	30	F	C	F	C	C	...	...	...	...	...	...	...	F	...	...	...	...
			3	C	C	F	...	F	...	...	...	...	...	R	...	...	...	...	...	...
"	76	...	87	C	A	R	R	R	...	...	C	...	...	F	C	R	...	...	...	...
			3	C	C	F	...	...	...	...	...	...	...	...	...	...	...	...	...	...
"	77	...	55	C	C	R	...	R	...	...	C	...	...	F	C	...	...	...	...	...
			3	C	C	C	...	...	...	...	F	...	...	...	...	...	...	...	...	...
"	78	...	38	F	A	R	F	C	e	...	F	...	...	...	F	Ri	...	...	...	...
			3	...	A	C	...	F	...	...	...	...	...	...	...	...	...	...	...	...

TABLE C. Copepods taken at Masset Inlet Station 89, July 24, 1953. (A—abundant; C—common; F—few; R—rare; i—immature; a—adults; the roman numerals I–V identify copepodite stages.) Following a comma, the word "to" is an abbreviation for "from younger stages up to".

Depth *m.*	Time	*Pseudocalanus minutus*	*Oithona helgolandica*	*Centropages mcmurrichi*	*Acartia clausi*	*Metridia lucens*	*Calanus finmarchicus*	*Oncaea conifera*
1	0015	C, i and ♀	C, i to a	F, i and ♀ ♂	F, to ♂	R, III	...	...
3	0045	C, i and ♀ ♂	C	C, ♀ ♂	F, to ♀ ♂	C, I to a	F, V	R, i and ♀ ♂
10	0130	C, i	C	F, V and ♂	R, to ♀ ♂	C, III to V	F, V	F, i and ♀ ♂
14	0200	C, ♀ ♂	C	...	...	C, II to a	F, V	C, ♀ ♂
25	0230	C, ♀ ♂	C	...	R, ♀	C, II to a	F, V	C, ♀ ♂
36	0245	R, ♀	C	...	R, ♀	C, i to ♂	F, V	C, ♀ ♂
50	0300	F, I and V	F	...	...	C, II to ♀ ♂	R, V	C, ♀ ♂
64	0310	F, I and V	R	...	R, ♀	C, II to ♂	F, V	C, eggs, i and ♀ ♂
82	0345	C	...	...	F	R	C, V	C?
74	0030	C	R	R	...	C	C, V	C?
74	0630	C	F	R	...	C	C, V	C, eggs
1	0805	C, to ♀ ♂	F, a	F, ♀	R, i and ♂	R, III	...	F, ♀ ♂
3	0815	C, to ♀ ♂	F, to ♀ ♂	R, ♂	R, i and ♀	R, III	...	C, ♀ ♂
10	0840	C, to ♀ ♂	C, to ♀ ♂	R, ♀	...	F, III to V	...	C, ♀ ♂
19	0900	C, to ♀ ♂	C, to ♀ ♂	...	...	F, III to V	...	C, ♀ ♂
30	0915	F, to ♀ ♂	C, to ♀ ♂	...	...	C, II to ♀	R, V	C, ♀ ♂
50	0930	R, to ♀ ♂	F, to ♀ ♂	...	...	C, to ♀ ♂	C, V to ♀	F, eggs ♀ ♂
74	0930	C, to ♀ ♂	F, to ♀ ♂	F, to ♀ ♂	R, ♀	C, to ♀ ♂	C, V to ♀	C, eggs, ♀ ♂

TABLE C (continued)

Depth *m.*	Time	*Pseudocalanus minutus*	*Oithona helgolandica*	*Centropages mcmurrichi*	*Acartia clausi*	*Metridia lucens*	*Calanus finmarchicus*	*Oncaea conifera*
1	1300	C, to ♀	C, to ♀ ♂	F, to ♀	R, ♂	R, I	...	R, ♀ ♂
3	1310	C, to ♀ ♂	C, i	F, to ♀ ♂	...	R, IV	...	R, ♀ ♂
10	1345	C, to ♀ ♂	C, to ♀ ♂	R, i	...	R, II V	...	C, ♀ ♂
14	1410	F, to ♀ ♂	C, to ♀ ♂	...	...	F, II III	...	C, ♀ ♂
25	1413	R, to ♀	C, to ♀ ♂	...	...	F, II III	...	C, ♀ ♂
36	1445	R, to ♀	C, to ♀	...	...	C, II to ♀ ♂	R, V	C, ♀ ♂
50	1455	R, to ♀	R—?	...	...	C, to ♂	C, V	C, ♀ ♂
64	1505	F, to ♀	R	...	...	C, to ♂	C, V	C, eggs and ♀ ♂
75	1530	A	F	R, ♀	R, ♀	C, to ♂	A	C, eggs and ♀ ♂
1	1820	C, to ♀ ♂	F, to ♀ ♂	F, to ♀ ♂	R, ♂	R, III	...	R, ♂
3	1840	C, to ♀ ♂	F, to ♀ ♂	F, ♀	R, ♀	R, III	...	R, ♀
10	1845	C, to ♀ ♂	C, to ♀ ♂	...	...	R, III to IV	...	F, ♀ ♂
20	1900	F, to ♀ ♂	C, to ♀ ♂	...	...	R, III to IV	...	C, ♀ ♂
30	1915	R, to ♀	C, to ♀ ♂	...	...	C, I to ♀	R, IV	C, ♀ ♂
50	1925	R	F	...	...	C, to ♀ ♂	F, V	C, eggs and ♀ ♂
75	1830	C	C	F	...	C	C	C, eggs and ♀ ♂

TABLE B. Occurrence of the less common copepods. The first number of each group is the number of the station where the species was taken; following it in brackets are the depth of the haul in meters, and the abundance of individuals taken rated according to the symbols described in Table A.

Eurytemora hirundoides	73(3, R); 91(27, R); 92(8, F)
Microsetella rosea	99(91, R); 82(206, R); 83(364, F); 94(55, R); 122(95, R); 127(14, C)
Bradyidius similis(?)	127(50, F); Adam Rock(120, R)
Calanus cristatus	81(?, R); 83(364, R); 86(91, R); 118(347, R); 124(643, R)
Calanus tonsus	83(364, R); 86(91, R); 114(164, R); 118(347, R); Adam Rock(120, R)
Euchaeta japonica	83,(364, R); 118(347, R); 124(643, R)
Candacia columbiae	83(364, R); 124(643, R)
Pleuromamma sp.	83(364, R); 124(643, R)
Heterorhabdus sp.	83(364, R); 124(643, R)
Gaetanus sp.	83(364, R); 124(643, R)
Clausocalanus acuicornis	114(164, R)
Metridia longa	83(364, C)
Chiridius sp.	83(364, R); 111(119, R); 118(347, C); 124(643, F)
Scolecithricella subdentata	124(643, R)

TABLE D. The age proportions of copepodite stages of *Metridia lucens* and *Calanus finmarchicus* in Masset Inlet.

Station	I	II	III	IV	V	♀	♂
			Metridia lucens				
74	8	6	2	1			
75	13	9	1	6	1		
76	28	18	6	3	2	1	
77	27	10	4	3	11	3	5
78	21	9	5	...	3	...	1
			Calanus finmarchicus				
75	...	...	...	...	1		
76	...	...	...	...	4	1	
77	...	...	...	...	10	...	

Scale Characteristics of Yearling Coastal Cutthroat and Steelhead Trout[1]

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ABSTRACT

Some scale characteristics of 88 yearling coastal cutthroat trout (*Salmo clarki clarki*) and 96 yearling steelhead (*Salmo gairdneri*) were compared in some detail. Although the number of diagonal scale rows above the lateral line was significantly higher in cutthroat, the counts of the two species overlap. The correlation of scale circuli counts with scale diameter was 0.94 for steelhead and 0.90 for cutthroat. At any given scale size cutthroat had 8 per cent more circuli than steelhead scales. Measurements of lateral and longitudinal diameters and anterior radii of scales show that the anterior portions of cutthroat scales tend to be longer and narrower than those of steelhead.

Regression analyses of each scale measurement on fork length indicated that, for any given fork length, cutthroat scales are smaller than those of steelhead; the greatest difference being apparent when anterior radii are compared. Growth of scales in a dorsoventral plane approximates isauxesis in relation to fork length but scale growth in a longitudinal plane tends toward positive heterauxesis which is particularly pronounced in the anterior portions of scales.

Multiple regression analyses of scale diameter, scale row count and fork length indicated that the smaller size of cutthroat scales is not balanced by proportionate increase in their number. When scale diameter is adjusted for scale number and fork length, cutthroat scales are 15.6 per cent smaller than those of steelhead, indicating that young cutthroat are covered by their scales with less overlap.

INTRODUCTION

The identification of the sea-run variety of *Salmo gairdneri* (steelhead) and the coastal cutthroat *Salmo clarki clarki* can be difficult, especially when the two species occur together. In older fish hyoid teeth, mouth size, and colour characteristics readily separate the species; however, these characteristics are not sufficiently developed in the younger and smaller fish to be useful for purposes of identification. It has often been noted, while making age determinations, that the scales of cutthroat and steelhead trout appeared to differ, both with respect to shape and size. If this apparent difference proved to be a significant one in young fish, then the difference could be useful as an identification tool. For this reason a detailed study of the scale characteristics of under-yearling steelhead and cutthroat trout was undertaken.

Fish samples consisting of 88 cutthroat and 96 steelhead were taken from Cultus Lake hatchery. These samples form the bases for all comparisons in this study. The cutthroat originated from the hatchery's brood stock, were sampled in January 1954 at an age of nine months, and averaged 81.1 millimeters in fork

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length with a range of 52–117 millimeters. The sampled steelhead came to the Cultus Lake hatchery as "eyed" eggs from the South Tacoma hatchery (State of Washington), the eggs originating from the Chambers Creek run. These steelhead, sampled in January 1954 at an age of ten months, averaged 87.5 millimeters in fork length with a range of 58–159 millimeters. The cutthroat eggs held at the Cultus Lake hatchery were incubated at a mean temperature of 41°F; while the steelhead eggs from Tacoma, to the "eyed" stage, were incubated at a temperature of 56°F. Following the "eyed" stage the temperature history of both species was identical.

We wish to acknowledge the contribution rendered by Fishery Officer F. Pells and Hatchery Officer J. C. Lyons of the Cultus Lake hatchery, in providing the fish necessary for this study.

SCALE COUNTS

Although lateral line scale counts provide little basis for separation of closely related species within Salmonidae, it has been shown (Neave, 1943) that counts of oblique rows dorsad to the lateral line could be useful in separating certain populations of cutthroat and steelhead trout. This might result from differences

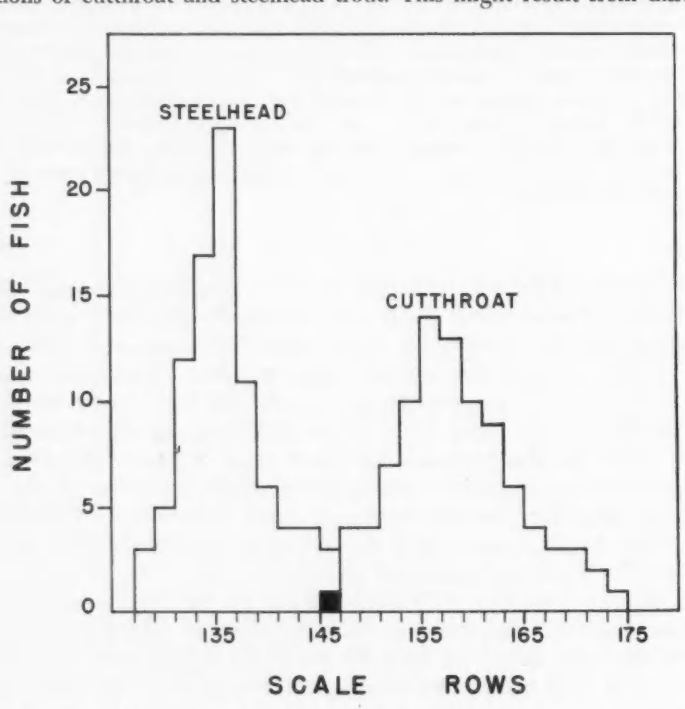

FIGURE 1. Distribution of scale-row counts in steelhead and coastal cutthroat trout.

between salmonids in the degree of branching of oblique scale rows above the lateral line. In the following study, counts were made of the number of oblique rows of scales 4 rows above the lateral line, from the gill aperture to the tip of the caudal peduncle. Crowding of scales towards the tip of the peduncle often made it difficult to enumerate, within two or three, the total number of rows. This was especially true in the case of the smaller individuals of the sample.

Figure 1 summarizes the results of the scale row counts. Mean value for steelhead was 136 and for cutthroat 158. With the exception of a single cutthroat which exhibited a scale count of 146, there was no overlap of the two ranges; steelhead 127–147 and cutthroat 146–173. These results are sufficiently discrete that almost all cutthroat and steelhead, reared at the Cultus Lake hatchery under similar conditions of temperature, and originating from these particular stocks,

TABLE I. Number of oblique scale rows above the lateral line of steelhead and coastal cutthroat in British Columbia.

Species	Locality	Mean count	Range	Authority
Cutthroat	Cowichan Hatchery	160.4	146–177	Neave, 1943
"	Veitch Hatchery	137.4	122–154	Neave, 1943
"	Not stated		143–180	Dymond, 1932
"	Not stated		170–200	Carl & Clemens, 1953
Steelhead	Cowichan Hatchery	131.5	123–143	Neave, 1943
"	Cowichan River	132.2	123–141	Neave, 1943
"	Not stated		124–146	Dymond, 1932
"	Not stated		115–159	Carl & Clemens, 1953

can be separated on scale row count alone. Table I lists some previously published scale row counts of steelhead and coastal cutthroat. From this table it can be seen that mean scale row counts of cutthroat are consistently higher than those of steelhead, and also that the range of variation is about 50 per cent greater than that of steelhead. Scale row counts of the present samples are in accord with previous work except for the cutthroat scale row counts of Carl and Clemens (1953). The latter counts appear aberrant in that both upper and lower limits of the range are higher than found by other workers.

It is generally known that meristic features such as scale rows may be affected by both hereditary and environmental factors. Although these factors may combine in certain streams, as they have in the present instance, to produce more or less clear-cut differences in scale row counts between steelhead and coastal cutthroat, these differences are not of general value in separating these species. In many cases the counts of one species overlap those of the other.

SCALE MEASUREMENT METHODS

Scales were removed from the area above the lateral line and posterior to the dorsal fin, washed in water and mounted with a solution of Canada Balsam crystals and dioxane on glass slides. The slides were examined and the scales measured under a monocular microscope fitted with an ocular micrometer. Longitudinal and lateral diameters were measured through the scale focus while

anterior radii were measured from the focus center to the anterior margin. Circuli were counted on the anterior portion of scales along radii with minimum numbers of broken circuli. The various measurements and the circuli counting area are illustrated in Figure 2.

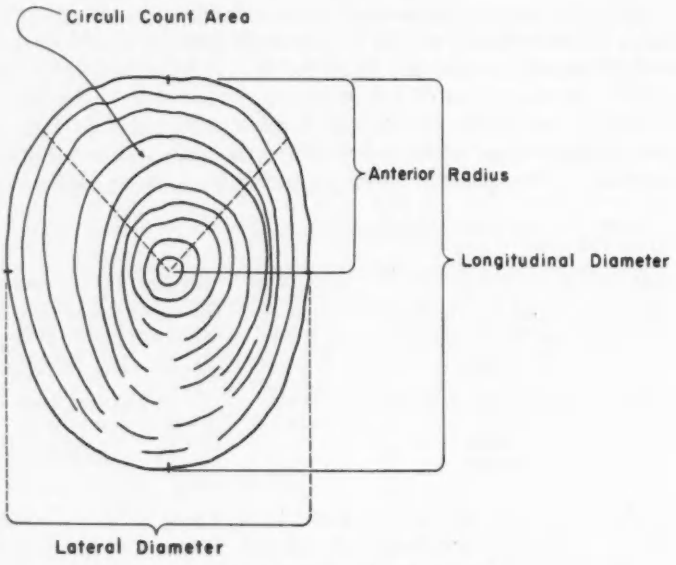

FIGURE 2. Measurements made on scales.

All counts and measurements represent the arithmetic means of five scales chosen at random from each slide. Broken and regenerated scales were rejected. For ease of calculation and avoidance of fractions, scale measurements were not transposed from micrometer units to metric units. Micrometer units may be transposed to millimeters by dividing the former by 138.89.

CIRCULI

The relation of the number of scale circuli to scale diameter is illustrated in Figure 3. The correlation is very high, the coefficient being 0.94 for steelhead and 0.90 for cutthroat. Thus circuli counts might be utilized as approximations of scale size in growth-rate studies of young trout.

From the calculated regression equation for each species, circuli counts were adjusted to a combined mean lateral scale diameter of 68.9 micrometer units. At this value the mean circuli count for steelhead was 11.75 $\pm$ 0.17, and 12.65 $\pm$ 0.19 for cutthroat. This difference is significant ($P < .01$). Thus at a given scale size, young cutthroat have an average of 8 per cent more circuli than steelhead. Conversely, steelhead have more widely spaced circuli.

LATERAL SCALE DIAMETER (SCALE UNITS)

FIGU

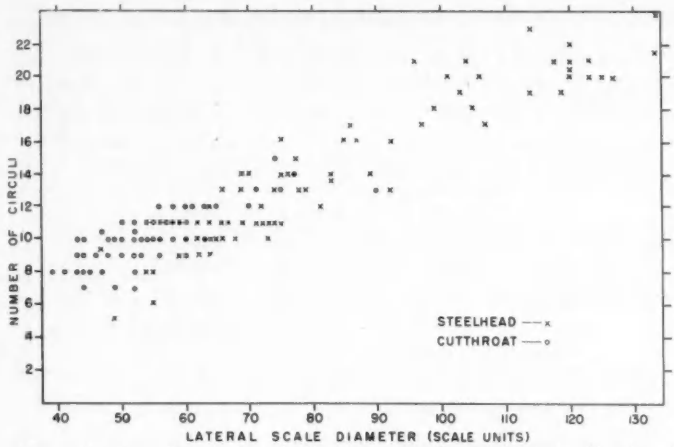

FIGURE 3. The relation of scale diameter to scale circuli in steelhead and cutthroat.

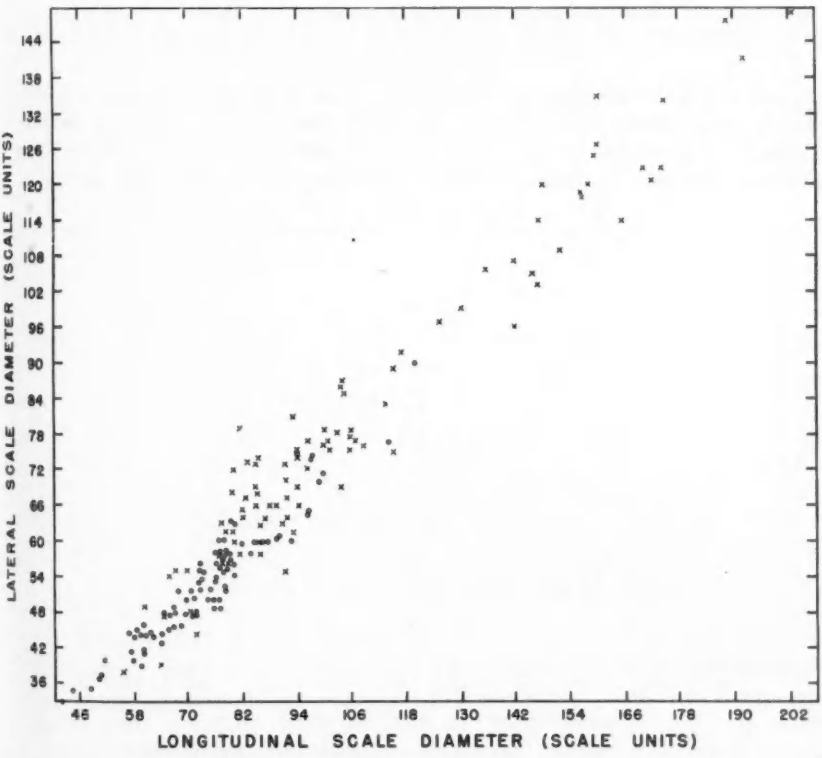

FIGURE 4. The relation of lateral scale diameter and longitudinal scale diameter. Circles—cutthroat; crosses—steelhead.

SCALE SHAPE

During examination of scales, the impression was formed that cutthroat scales tended to be narrower than those of steelhead. However, the plots of lateral diameter on longitudinal diameter (Fig. 4) indicate no significant difference in these proportions between the species at the ages sampled. However, the ratio of mean lateral diameter to mean longitudinal diameter (Table II) is 0.76 for

TABLE II. Mean scale dimensions and proportions of steelhead and cutthroat.

Scale characteristics	Steelhead	Cutthroat
Mean longitudinal diameter (a)	110.24	73.49
Mean lateral diameter (b)	83.80	52.57
Mean anterior radius (c)	52.97	36.66
Ratio of lateral diam. to longitudinal diam. (b/a)	0.76	0.71
Ratio of anterior radius to longitudinal diam. (c/a)	0.48	0.50
Ratio of anterior radius to lateral diam. (c/b)	0.63	0.70
Anterior radius adjusted to common lateral diameter by regression equations	39.02±1.011	45.25±1.012

steelhead and 0.71 for cutthroat. This difference of 6 per cent suggests a slight tendency for steelhead scales to be more nearly circular than cutthroat scales.

The plots of anterior radius and longitudinal diameter similarly indicated no significant difference in these proportions, between species. The ratio of mean

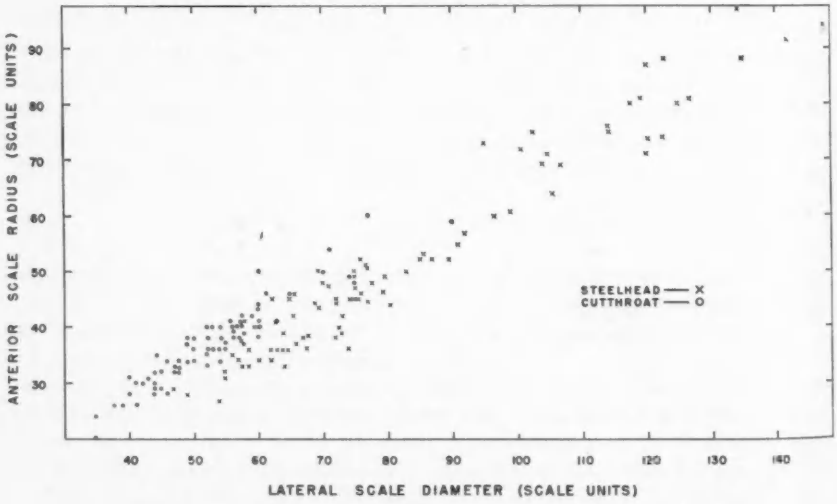

FIGURE 5. The relation of anterior scale radius and lateral scale diameter.

anterior radius to mean longitudinal diameter (Table II) is 0.48 for steelhead and 0.50 for cutthroat—a difference of 4 per cent. Thus foci of cutthroat scales tend to be in the centre of the longitudinal axis while foci of steelhead scales are displaced slightly anteriorly with a consequent shortening of the anterior portions of the scales.

These small differences in scale shape combine to magnify the difference between species in the ratio of anterior radius to lateral diameter (Fig. 5). The ratio is 0.63 for steelhead and 0.70 for cutthroat—a difference of 11 per cent (Table II). Thus steelhead scales are more nearly circular, the anterior radii are slightly shorter and as a consequence the anterior portions of cutthroat scales tend to be longer and narrower than those of steelhead. This is illustrated diagramatically in Figure 6.

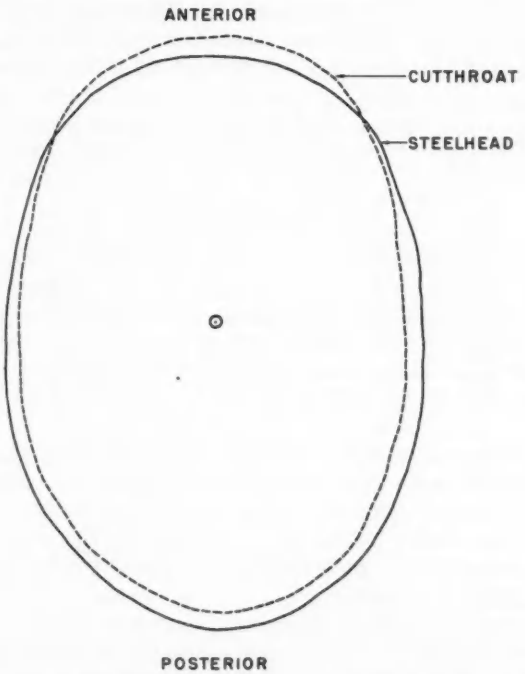

FIGURE 6. Diagrammatic representation of steelhead and cutthroat scales of similar length, superimposed with foci aligned.

A regression analysis indicated that when the anterior scale radii were adjusted to a common lateral diameter of 64.4 micrometer units (geometric mean) the mean anterior radius was 45 ± 1.01 micrometer units for cutthroat and 39.0 ± 1.01 micrometer units for steelhead. Thus differences between scales of steelhead and cutthroat in the ratios of the two diameters and in the ratios of

anterior radii to longitudinal diameters are too small to be statistically significant when considered separately. However, these small differences augment each other to produce a significant ($P < .01$) difference in the shape of anterior portions of steelhead and cutthroat scales.

THE RELATION OF SCALE SIZE TO FORK LENGTH

It has been noted that three separate measurements were made on each scale—longitudinal and lateral diameters and anterior radius. To make all possible comparisons between the two species, and also to examine the usefulness of these various measurements, a regression analysis of each measurement on fork length was made.

To adjust for any tendency toward a curvilinear relationship between scale size and fork length, and also to adjust for a slight tendency for variance to be proportional to the mean, logarithmic values were used in the regression analysis. Pertinent regression statistics are listed in Table III. No significant differences of

TABLE III. Regression statistics of scale size and fork length. (To assess differences between species all scale measurements were adjusted to a grand mean fork length of 83.1 mm.)

Scale measurement	Statistic	Steelhead	Cutthroat
Longitudinal diameter	Slope (b_{yx})	1.1079	1.0655
	Standard error of slope	0.0389	0.0185
	Scale size at 83.1 mm. F.L.	102.2±1.008	74.46±1.019
Anterior radius	Slope (b_{yx})	1.2530	1.1529
	Standard error of slope	0.0334	0.0221
	Scale size at 83.1 mm. F.L.	48.26±1.009	37.11±1.008
Lateral diameter	Slope (b_{yx})	1.0636	1.0194
	Standard error of slope	0.0414	0.0211
	Scale size at 83.1 mm. F.L.	78.01±1.009	50.32±1.016

regression coefficients were found between species. When scale size is adjusted to a common fork length (the geometric mean, 83.1 mm.) highly significant differences are apparent between species. In all cases cutthroat were found to have smaller scales than steelhead at a given length. The greatest difference in scale size is apparent when anterior radii are compared, reflecting the difference in scale shape noted previously.

A tendency toward positive heterauxesis in growth of these scales in relation to fork length is indicated by the fact that values for the slopes (b_{yx}) are in each case greater than unity. Scales are growing at a slightly greater rate than fork length. The slope of lateral diameter most clearly approximates unity in both species, while slopes of anterior radii show the greatest departures from unity.

Since fork length is a longitudinal measurement it would appear most logical to use a longitudinal scale measurement when describing the relation of scale growth to body length. However, it has been shown that for young fish of these species a lateral (dorso-ventral) scale measurement most closely approximates proportional growth.

Smith (1955) found a very high degree of positive heterauxesis in lateral growth of scales from young Kamloops trout (*Salmo gairdneri*) with a sharp inflection at a fork length of 45 millimeters, followed by proportional growth. He suggested that this high initial relative growth rate occurred during the period immediately following scale formation and continued until the normal degree of scale overlap had been attained.

The smallest fish examined in the present paper was 52 millimeters in fork length—well above the area of inflection found by Smith. In the present case it is suggested that the scale-bearing or trunk section of these fish is growing faster than total or fork length and that, longitudinally, scales are growing proportionately to the scale-bearing length. It is generally known (Martin, 1949) that, in salmonids, relative growth rates of heads is reduced after a standard length of 30–35 millimeters is reached. Conversely, the relative growth rate of scale-bearing or trunk length must increase for a period after this inflection point.

The hypothesis that longitudinal scale growth is proportional to scale-bearing length requires testing. On the basis of the present data and previous work it would appear that lateral scale measurements most closely approximate isauxesis or proportional growth and are more useful in calculation lengths previous to capture, when fork length measurements are used.

ADJUSTED SCALE SIZE

It has been shown that at any given fork length, cutthroat scales are smaller than those of steelhead. Also it has been shown that cutthroat have a greater number of scales between the operculum and caudal fin. Thus the scale-bearing length is divided among a larger number of scales in the case of the cutthroat, and it might be assumed that the decrease in scale size would be proportional to the increase in the number of scales. To test this assumption a multiple regression analysis was made, following procedures outlined by Snedecor (1946).

With Y designated as longitudinal scale diameter, X_1 as fork length and X_2 as scale-row count, the following multiple regression equations were calculated:

$$\text{Steelhead: } Y = 47 + 14X_1 - 0.47X_2$$
$$\text{Cutthroat: } Y = 39 + 10X_1 - 0.39X_2$$

By introducing grand mean values of X_1 and X_2 ($\overline{X}_1 = 8.43$ centimeters and $\overline{X}_2 = 147.05$ micrometer units) into each of these equations the following values of adjusted longitudinal scale diameter may be derived:

Steelhead: 95.9 micrometer units
Cutthroat: 80.7 micrometer units
Difference: 15.2 micrometer units.

Thus when longitudinal scale diameter is adjusted for fork length and for scale number, cutthroat have scales 15.8 per cent smaller than steelhead. This difference in scale size is significant ($P < .01$). The larger number of scales of cutthroat does not account for all the difference in scale size.

To indicate the effects of fork length and scale count on scale size within species, partial correlation coefficients were calculated. The correlation of scale size and fork length, independent of scale number ($r_{Y1.2}$), was 0.9667 ($P < .01$) for steelhead and 0.9391 ($P < .01$) for cutthroat. The correlation of scale size and scale count, independent of fork length ($r_{Y2.1}$), was –0.231 ($P < .05$) for steelhead and –0.3505 ($P < .01$) for cutthroat. Total correlation (R) was 0.970 ($P < .01$) for steelhead and 0.9393 ($P < .01$) for cutthroat. It can be noted that within each species $r_{Y1.2}$ approximates R. Thus within species, scale size is directly dependent on fork length, and adjustment for scale number adds only slightly to the accuracy of estimating scale size.

Because of the complexity of the method and overlap of individuals, the adjusted scale size is not a useful anatomic feature for ready separation of the two species, of the sizes represented in the samples. However, it represents a real difference between species and indicates that young cutthroat are covered by their scales with less overlap than are young steelhead.

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On the Distinctness and Origin of the Slope Water off the Scotian Shelf and its Easterly Flow South of the Grand Banks[1,2]

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ABSTRACT

The Slope Water south of Nova Scotia lies as a distinct water mass between Coastal Water and the Gulf Stream. A characteristic temperature–salinity correlation exists. Although the T–S curve lies close to that for Central Atlantic Water, if a reasonable system of mixing is assumed, the composition is shown to be Atlantic Water diluted by the addition of approximately 20% of Coastal Water. The rate of production of Slope Water is estimated to be of the order of 2×10^7 m.^{3}/sec. and the observed eastward flow carries this mixing product from the area of formation. A secondary current in the Gulf Stream system is thus generated by means other than simple bifurcation of the main stream. Such a current has been consistently observed.

INTRODUCTION

Within some 250 miles of the Nova Scotia coast three distinctly different oceanographic regions are found. In sequence from the coast, they are the Coastal Water, the Slope Water and the waters of the Gulf Stream. The transition from one region to the next is not a gradual one, but involves the crossing of sharp boundaries where, within a very few miles, large variations in temperature and salinity take place.

Temporal variations and other features of the Slope Water have been discussed by McLellan *et al.* (1953). In that paper vertical temperature distribution was shown in section for each of six crossings from a two-ship survey carried out in November 1951. In the continuing project for the investigation of the Slope Water extensive surveys were also carried out in June 1952 and August 1953 when observations of temperature and salinity were made over wide networks and supplemented with electro-magnetic current measurements. McLellan (1956, fig. 2) has shown the vertical temperature distribution from a section running south from the Grand Banks on June 25 to 27, 1952, in which the division into three regions is most distinctly shown.

It is proposed herein to discuss the origin of the Slope Water and persistent currents within it based on the results of these surveys.

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[2]This paper is taken from a dissertation presented in partial fulfilment of the requirements for the degree Doctor of Philosophy in Physical Oceanography at the University of California, Los Angeles.

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I. Characteristics and Origin of Slope Water

The plotted vertical temperature distribution for any section running from Coastal Water to the Gulf Stream shows that, from its temperature–depth relationship alone, the Slope Water forms a distinctive band of waters. This distinctness holds to at least 250 m. The temperature–depth relationship in a water column, however, shows very little concerning the probable origin of the waters. It is necessary to examine the temperature–salinity (T–S) relationships to gain some insight into the nature of the water mass. In this respect, it is convenient to consider separately a surface layer and the deeper waters. The limiting depth of the surface layer is not always definite but is usually designated as that depth below which wind stirring and solar heating produce negligible seasonal variation. This depth is usually between 150 and 200 m.

Characteristics of the surface layer of the Slope Water

As they do geographically, so on a T–S plot the waters of the surface layer in the Slope Water lie intermediate between the Coastal Waters and those of the Gulf Stream. This has been shown by McLellan *et al.* (1953) to hold for the observations from the November 1951 cruise, and is seen again in Fig. 1 depicting the scatter of points representative of waters in the upper 150 metres at twenty-two stations occupied during June 1952. The locations of these stations are given in Table I.

Table I. Locations of Hydrographic Stations occupied during June 1952.

Station	N. Latitude	W. Longitude
129	40°40.5′	57°20′
132	41 29	57 30
134	42 12	57 28
136	42 52.5	57 30
138	43 21	57 30
139	43 37	57 27
140	43 53	57 23
141	44 06.5	57 30
142	44 19	57 29
225	39 32.5	51 54
226	40 02.5	52 09
227	40 18	52 18
228	40 36	52 23
229	41 17	52 24.5
230	41 56	52 25
231	42 25	52 30
232	42 48	52 30
233	43 08	52 30
234	43 30	52 30
235	43 51.5	52 30
236	44 05	52 30
237	44 20	52 30

Ten of these stations were occupied within the coastal regime, nine in the Slope Water, two in the Gulf Stream, and one in a warm eddy within the Slope Water region.

During this cruise an attempt was made to obtain observations close to the boundaries. This was accomplished by sailing south carrying a temperature plot from bathythermograph (BT) observations, then returning north occupying stations at the indicated locations. It was felt that this technique might show a complete gradation in the properties of the waters. However, the data, when presented on a T–S plot as in Fig. 1, fall into three distinct groups. Each group

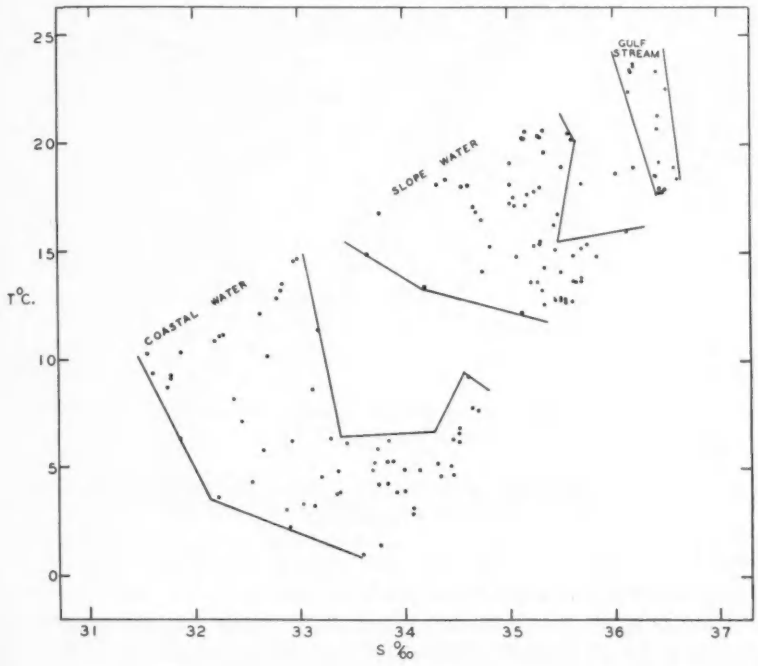

FIG. 1. T–S relations in the upper 150 m. as observed during June 1952.

has been indicated by bounding lines and it may be remarked that the areas occupied by these groups on the T–S plot do not overlap. There are indeed blank areas separating them, into which no observations fall. The points falling between the Gulf Stream and Slope Water areas represent surface water from the warm eddy within the Slope Water. This is further shown by Fig. 2 where the T–S curves for the upper layers at selected stations are shown. Station 136 was in a warm eddy located between stations 134 and 138. Station 129 was a Gulf Stream station on the same line. It can be seen that water from the upper 25 to 50 m. within the eddy had become measurably mixed with Slope Water.

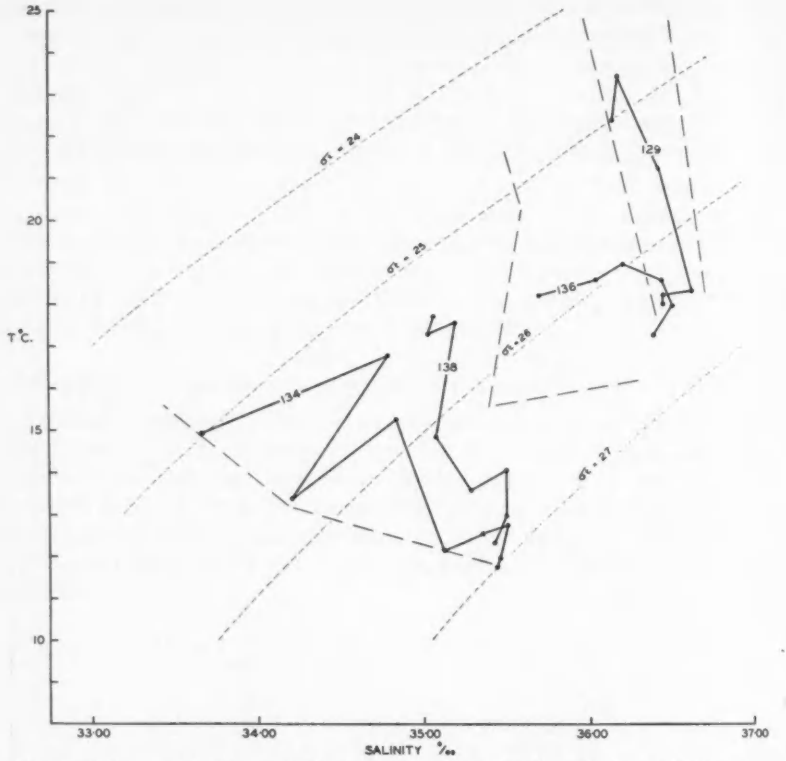

FIG. 2. T–S curves for the upper layers at selected stations from the June 1952 cruise.

ORIGIN OF THE SURFACE LAYER OF THE SLOPE WATER

It would appear from the data portrayed in Fig. 1 that the upper layers of the Slope Water are formed by the mixture of discrete quantities of Gulf Stream and Coastal Waters and that the proportions involved vary from 50% of each to 75% Gulf Stream and 25% Coastal Water. The segregation of the waters into distinct classes signifies that all three water types are formed outside the area of observations and that any mixing which takes place between adjacent waters is confined to extremely narrow bands such that the intermediate products are not usually observed.

From the results of the November 1951 cruise, McLellan *et al.* (1953) were led to believe that in the upper layers mixing took place between Coastal and Gulf Stream waters from the same depths. This postulate is further investigated in Fig. 3. In this diagram T–S plots are shown for stations 225, 229 and 232 of *Sackville* cruise 8 in June 1952. These stations are representative of Gulf Stream, Slope Water and Coastal Waters, respectively. Points representing observations at like depths at the three stations have been joined in the diagram.

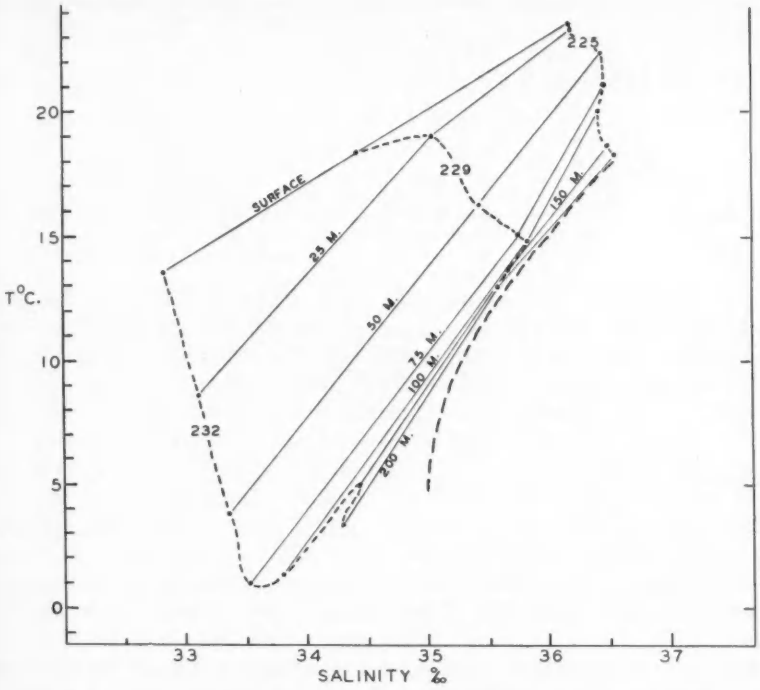

FIG. 3. T–S relationships in the upper layers at three stations occupied during June 1952. Observations at like depths are joined by light solid lines.

The theory of horizontal mixing is supported by the fact that the surface and 50-m. observations fall on straight lines in the diagram and the observations at other depths do not depart greatly from a straight-line relationship. The Slope Water observations from 100, 150 and 200 m. fall on a line paralleling part of the Central Atlantic curve (dashed line to right of Figure). This line coincides with the mixing line for 150 m., and might well indicate the operation of a system of mixing and sinking, giving rise to the Slope Water of intermediate depths.

CHARACTERISTICS OF THE DEEPER SLOPE WATER

(A) TEMPERATURE AND SALINITY. In Fig. 4, a composite T–S curve for the Slope Water deeper than 150 m. has been constructed. Data from all stations occupied during *Sackville* cruises 3 and 8 in November 1951 and June 1952 were used in arriving at this curve. All of the observations were plotted and a curve of visual best fit was drawn through the points. In Fig. 4 are also shown the curve for Central Atlantic Waters (Iselin, 1936, fig. 22), the curve for Labrador Current waters (Soule, 1940b, fig. 28), a curve representative of Coastal Waters and the curve for Mixed Water (Soule, 1951). The approximate depths at which waters

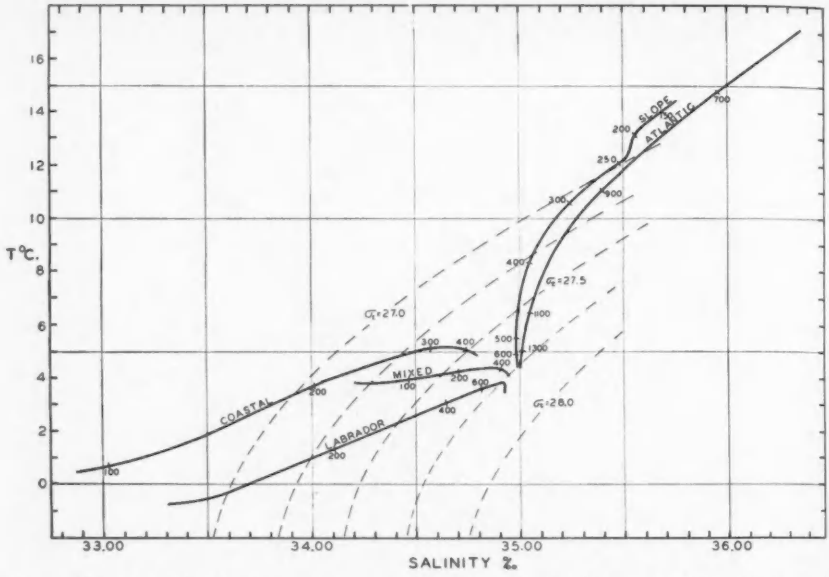

FIG. 4. T–S curves for five water masses found between the Gulf Stream and the Continental Shelf and between longitude 45° and 65°W. Approximate depths in metres are indicated.

of the various characteristics are found have been indicated on the curves. Almost all observations from the Slope Water region between longitudes 50°W. and 65°W. fell along the composite curve given in Fig. 4 within the error of observation. An occasional water sample was found to deviate to such an extent that an abnormal admixture of Coastal or Gulf Stream Water was signified. In no case, however, did Slope Water samples show characteristics which did not fall measurably to the left of the Central Atlantic curve.

The Slope Water curves regularly show a definite inflection with a closest approach to the Central Atlantic curve at some depth around 250 m., where the temperature is approximately 12°C. For depths greater than 250 m., and as great as 600 m., the maximum depth of observation at most of the stations, the curve bears a relationship to the Central Atlantic curve similar to that found by Iselin (1936, fig. 23). The differences in salinity for any temperature in these observations is, however, somewhat greater than that found by Iselin. This difference may simply result from the fact that most of the observations here considered were made at locations northeast of the area of Iselin's observations. A greater Coastal Water influence is indicated.

(B) DISSOLVED OXYGEN. At some of the stations occupied during the June 1952 cruise, measurements of dissolved oxygen were made. The results from stations 225, 230 and 231 are given in Table II as typical of observations from Gulf Stream, Slope Water and Coastal Water, respectively.

TABLE II. Dissolved oxygen at three stations occupied during the June 1952 cruise.

Depth	Station 225 (Gulf Stream)	Station 230 (Slope Water)	Station 231 (Coastal Water)
m.	*ml./l.*	*ml./l.*	*ml./l.*
100	4.9	4.4	6.3
150	5.0	4.8	6.5
200	4.7	4.1	5.5
300	4.7	3.9	5.7
400	—	3.3	6.1
500	—	3.9	6.1

All stations in the Slope Water at which observations were made showed oxygen minima of between 3.3 and 3.9 ml./l. at depths from 250 to 400 m. At similar depths (300 m.) at Gulf Stream and Coastal Water stations values were respectively about 4.3 and 6.0 ml./l. The low value of dissolved oxygen at this level in the Slope Water corresponds closely to values found by Seiwell (1934) in the oxygen-minimum layer in the Western Basin of the North Atlantic. Seiwell found this oxygen-minimum layer at depths of from 750 to 1,000 m. The implication is that the main constituent of Slope Water from this depth is Atlantic Water identical to that found at much greater depths south and east of the Gulf Stream although the possibility that other factors are operative to produce this oxygen minimum is not excluded. The similarity in characteristics of the Slope Water and Atlantic Water, but from quite different depths, is shown in Fig. 4 and lends credence to the implication of the oxygen observations. The surfaces of constant properties must slope steeply upward from east to west under the Gulf Stream as a consequence of the strong current.

(c) DISTINCTNESS OF THE DEEPER SLOPE WATER. There does not seem to be complete agreement on the question of whether the subsurface Slope Water constitutes a distinct water mass or whether it merely represents a body of Atlantic Water which has been ejected from the Gulf Stream in accordance with the dynamic requirements formulated by Rossby (1936).

Iselin (1936) showed in his data two distinct sets of observations each falling along its own distinctive curve on a T–S diagram, with scatter that could be attributed to the errors in determining temperature and salinity. He reported waters from the Slope Water and Central Atlantic, with similar temperatures, differing in salinity by from 0.04‰ to 0.02‰. On comparing these curves, Rossby (1936) has said "there is fairly good agreement between the two sets of data, showing that coastal and northerly waters play a minor role in the production of Slope Water". In the same range of temperatures, the Slope Water curve obtained in the present investigations shows Slope Water and Central Atlantic Water, with similar temperatures, differing in salinity by from 0.10‰ to 0.05‰. This difference in salinity would indicate very little dilution if Central Atlantic Waters were being mixed with fresher waters of the same temperature. No such waters are available, however, and the mixture with waters known to exist must be considered.

Pollak (1947) has introduced a much more realistic criterion for examining the relationship of the two waters. Accepting the concept that mixing in the sea takes place along lines of equal potential density, he constructed a standard σ_t–S curve[3] for Central Atlantic Water and proceeded to plot deviations from the standard salinity against σ_t for a number of sections running from the continental shelf to the Gulf Stream. He was not convinced of the existence of a Slope Water with distinctive characteristics. It may be noted that, in such a treatment, Slope Water with characteristics shown in Fig. 4 would show salinity deviations varying from –0.22 at $\sigma_t = 27.0$, to –0.06 at $\sigma_t = 27.6$.

It is of interest to postulate a Slope Water formed from the mixture of Central Atlantic Water and some other water with more or less distinctive characteristics, to impose generally accepted rules upon the nature of the mixing process imagined, and to determine the relative proportions of the constituents required. If, then, it appears that Slope Water represents Atlantic Water which is significantly diluted, its distinctness should be considered proven. Such an examination will be made below.

ORIGIN OF THE DEEPER SLOPE WATERS

(A) AVAILABLE CONSTITUENTS. Within the area between the Gulf Stream and the Continental Shelf, and between longitudes 45° and 65°W., at least five water masses, each with its own characteristic T–S relationship, may be recognized. Of these the Central Atlantic or Sargasso Water, which makes up the Gulf Stream, and Labrador Water, which flows into the area in the Labrador Current, may be regarded as the main types of source water. The only other contribution is made by land drainage, with the fresh water being mixed in the various estuaries to form a low-salinity surface layer which characterises the inshore waters. Where fresh water enters the sea a brackish surface layer is produced which overlies the more saline water. The interface becomes a layer of great stability which inhibits vertical mixing so that it is doubtful if this contribution of runoff ever shows its influence at depths greater than 100 m. It seems safe, then, to assume that the other three water masses are formed either directly or indirectly by the mixture of Central Atlantic and Labrador Waters. Another necessary condition, of course, if this assumption is to be justified, is that the remaining water masses have characteristics intermediate between the characteristics of the two primary sources. That this is indeed so, can be seen by reference to Fig. 4 wherein are shown T–S curves representative of the five water masses. These five curves, representative of Central Atlantic, Slope, Coastal, Mixed and Labrador Waters were obtained in the following way:

1. *Central Atlantic.* This curve is taken from Iselin (1936). He has shown it to hold for a large body of water in the Sargasso Sea with deviations only of the order of the errors involved in observation.

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[3] $\sigma_t = 10^3 (\rho_{s,t,o} - 1)$ where $\rho_{s,t,o}$ is the density of sea water with salinity s, temperature t and at atmospheric pressure.

2. *Slope Water.* This is a composite curve whose construction has been discussed above and which represents Slope Water off the Scotian Shelf. Its variations from the Central Atlantic curve are similar in form to those for the Slope Water curve given by Iselin (1936), but are slightly greater in magnitude. The implication is that Slope Water is less saline in the eastern sector than in the area southwest of Georges Bank. This Slope Water curve agrees very closely with the average curve for Atlantic Current Water between the years 1934 and 1941 as given by Soule (1951) for temperatures below 8°C.

3. *Coastal Water.* This curve was obtained from two stations occupied in Cabot Strait during November 1950. It differs from the constant curve found to represent the deep waters of the Gulf of St. Lawrence (Lauzier and Bailey, 1956) only in that it includes deeper observations showing the characteristic downward trend of the curve for salinities greater than 34.6‰. The relationship of this curve to the characteristics of waters found against the Scotian Shelf will be discussed below.

4. *Mixed Water.* This curve represents the average for the years 1934–1941 for a distinct body of water found east of the Grand Banks and south of Flemish Cap. It is taken from Soule (1951).

5. *Labrador Water.* The Labrador curve is also taken from Soule (1951) and represents average conditions from 1934–1941.

(B) MIXING PROCESSES IN THE OCEAN. One of the most useful concepts in descriptive oceanography is that introduced by Rossby (1936) which postulates water restrained to move along isopycnic surfaces. Its use in studying flow patterns has been demonstrated by Montgomery (1938) and by Parr (1938). These authors referred respectively to isentropic surfaces and isopycnic surfaces. Both actually used σ_t surfaces as a respectable approximation. Although this concept is valuable in oceanographic analysis, care must be taken to avoid such statements as "mixing takes place along isopycnic surfaces", or the careless use of the term "isentropic mixing" and "isopycnic mixing". The distinction between "stirring" and "mixing" as brought out by Eckart (1948) is important. Stirring obviously can, and probably always does, take place on surfaces of equal density, since low internal friction in the fluid makes hydrostatic equilibrium (or quasi-equilibrium) the only state admissible. The very nature of mixing, however, implies a change in entropy. At the same time, the physical nature of sea water is such that the mixing of waters of equal density is accompanied by an increase in density in the product (except for the trivial case where the original constituents are identical as to temperature and salinity).

It is true that where the ranges of temperature and salinity are small, as is the case in the waters off Southern California investigated by Sverdrup and Fleming (1941), no great error is introduced by assuming mixing along σ_t lines, because σ_t lines on the T–S diagram approximate to straight lines over the range employed. If one considers mixing of Labrador and Atlantic Waters, however, water types of similar density may differ by as much as 2.6 parts per thousand

in salinity and by as much as 15.3°C. in temperature. The product of such mixing could differ from the original constituents by as much as 0.27 in σ_t. In such a case, one may consider that mixing takes place between waters of equal density but it must be remembered that the products are represented by a straight line on the T–S plot and not by the curve of equal σ_t.

(c) A GRAPHICAL METHOD FOR STUDYING MIXING. The method which will be used here to study mixing and mixing products is illustrated in Fig. 5. Characteristic curves for the water masses involved are laid off on a T–S plot upon which are superimposed lines of equal σ_t. It will be assumed that mixture takes place only between waters of equal density. It will also be assumed that all the products of mixing of two water types *A* and *B* have characteristics represented by points on the straight line joining *A* and *B*. This can be simply shown if the small variations in specific heat are neglected.

While mixing along straight lines on the T–S diagram is a useful concept in studying vertical mixing, its application to horizontal mixing must be viewed with a certain amount of scepticism. It presupposes a stirring together of discrete quantities of water of types *A* and *B* and the subsequent modification of each of the constituents taking place at rates which would maintain equal densities to the point where complete mixing has been achieved. It would, perhaps, be more realistic to consider an infinitesimal modification of *B* towards *A*. The product would then be no longer eligible for mixture with *A* or *B* because of its increased density, so that the next infinitesimal change must come from mixing with water of slightly different characteristics than *A*. If this sort of mixing is visualized, the line *AB* only defines the low-density limit for mixing products involving *A* and *B*. For simplicity, the concept of straight-line mixing will be retained throughout this development.

In Fig. 5, the T–S curves for Atlantic Water, Slope Water and Labrador Water have been shown. If it is assumed that Labrador and Atlantic Waters of $\sigma_t = 27.0$ (*A* and *B*) mix along the line *AB*, the point *C* represents the product as it appears in the Slope Water. The particulars of these three water types are given below:

Water	S‰	T° C.	σ_t
A	33.57	–0.42	27.00
B	35.55	12.20	27.00
C	35.12	9.42	27.17

The relative quantities of A and *B* involved in *C* are given by the relative lengths of the sectors of *AB*, that is, $B/A = AC/BC = 3.57$ or, in terms of percentage, the percentage of *B* in *C* is given by $P_B(\%) = AC/AB \times 100 = 78\%$. Similarly water types *D* and *E* from Labrador and Atlantic Waters might mix to give water type *F* in the Slope Water.

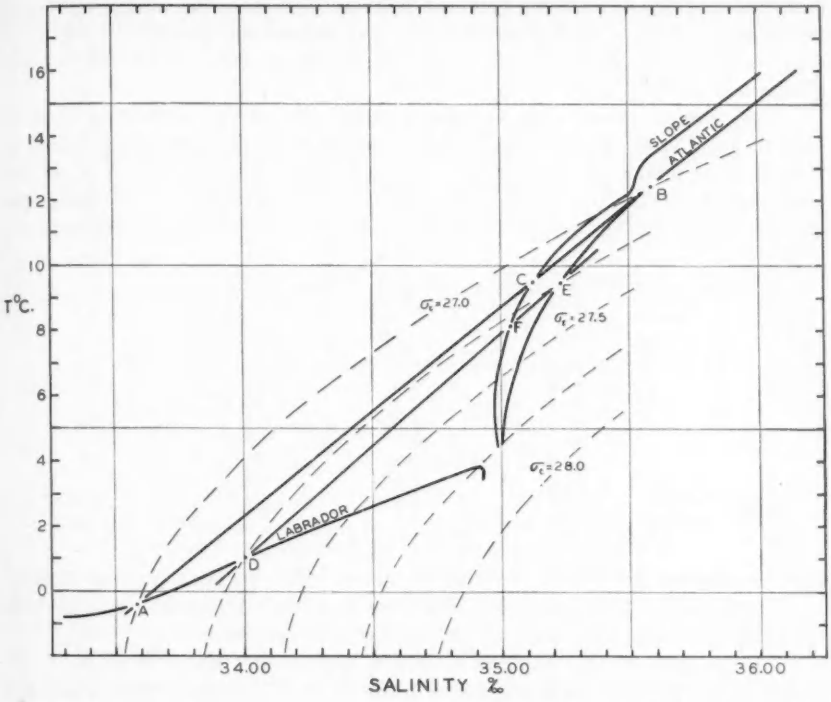

FIG. 5. T–S curves showing assumed mixing lines for the production of Slope Water from Central Atlantic and Labrador Waters.

(D) CONSTITUENT RATIOS IN SLOPE WATER. The method described above has been applied in evaluating the constituent ratios involved if the Slope Water were produced from the mixture of Atlantic and Labrador Waters. Whatever the intermediate steps, these must be the ultimate sources of Slope Water. The results are tabulated in Table III for each 0.1 interval in σ_t of the original

TABLE III. The constitution of Slope Water from Atlantic and Labrador Waters.

Initial	Atlantic		Labrador		Slope				
σ_t	S‰	T°C.	S‰	T°C.	S‰	T°C.	σ_t	$R=A/L$	P_A(%)
26.8	35.92	14.50	33.30	−0.80	35.23	10.48	27.07	2.77	74
26.9	35.72	13.30	33.43	−0.68	35.17	9.95	27.11	3.16	76
27.0	35.55	12.20	33.57	−0.42	35.12	9.42	27.17	3.57	78
27.1	35.41	11.08	33.73	0.06	35.09	9.00	27.21	4.30	81
27.2	35.27	9.93	33.90	0.65	35.06	8.43	27.26	5.27	84
27.3	35.18	8.90	34.07	1.20	35.03	7.81	27.33	6.30	86
27.4	35.12	7.88	34.24	1.78	35.01	7.10	27.43	6.90	87
27.5	35.08	7.02	34.42	2.36	34.99	6.40	27.52	6.60	87
27.6	35.04	6.10	34.61	2.90	34.98	5.60	27.61	6.00	86

constituents. The ratios are expressed both as $R = A/L$, the ratio of Atlantic to Labrador Waters and as $P_A(\%)$, the percentage of Atlantic Water. This analysis shows the Slope Water to be constituted of from 74 to 87% Atlantic Water.

Since comparatively little water with pure Labrador characteristics is found west of the Grand Banks, in the area where the formation of Slope Water is visualized as taking place, it is informative to make a similar analysis on the basis of Slope Water formation with Atlantic Water and Coastal Water as the basic constituents. The results of such an analysis are shown in Table IV. It

TABLE IV. The constitution of Slope Water from Atlantic and Coastal Waters.

Initial σ_t	$R = A/C$	$P_A(\%)$
26.7	3.8	79
26.8	4.8	83
26.9	3.9	80
27.0	3.6	78
27.1	3.6	78
27.2	3.8	79
27.3	3.6	78
27.4	3.3	77
27.5	2.7	73

must be pointed out that for mixture of waters with the same original density, the mixing lines will be quite different from those in the previous analysis and the relative increase in density of the product will be less.

On the basis of this analysis it would appear that the subsurface Slope Water off the Scotian Shelf consists of from 73 to 83% Atlantic Water and the constancy of the ratio for all values of σ_t is remarkable. What significance can be attached to this constancy is not immediately apparent, but it appears likely that Coastal and Atlantic Waters mix in fairly definite proportions throughout the whole column to produce the Slope Water as found in this area.

(E) CONSTITUENT RATIOS IN THE DEEPER COASTAL WATER. Coastal Water, from its geographical position as well as from the position of its characteristic curve upon the T–S plot (Fig. 4), must be formed by the mixture of Labrador and Slope Waters. The area of formation would be in the region immediately west of the Grand Banks.

Although the characteristic T–S curve in Fig. 4 has been used to represent Coastal Water, especially that found between the Continental Shelf and the Slope Water boundary, it is even more characteristic of the waters found in the Laurentian Channel and well into the Gulf of St. Lawrence. A large percentage of the hydrographic stations occupied in the region between the Continental Shelf and the Slope Water have had irregular T–S curves more or less of the nature of that shown in Fig. 6 for *Whitethroat* station WT-5-32A (lat. 43°43′N., long. 57°52′W.) occupied on November 11, 1950. The T–S curve oscillates about the standard curve, indicating a region where waters of different origin have been stirred together and where mixing has not been completed.

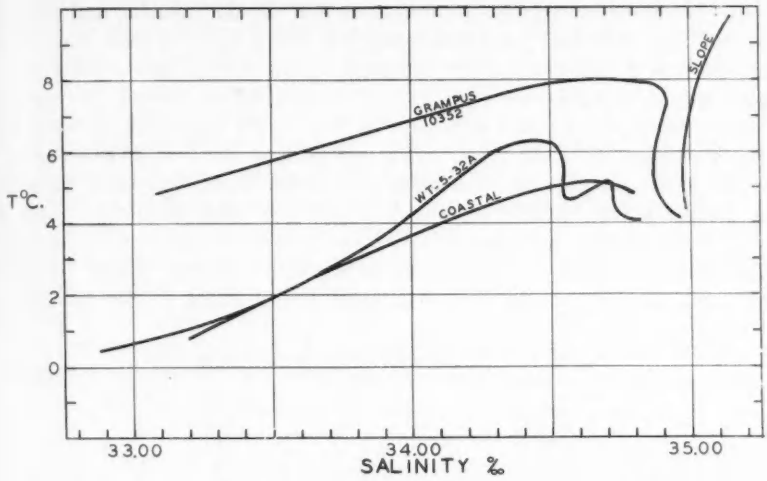

FIG. 6. T–S curves for station WT–5–32A, lat. 43°43′N., long. 57°52′W., Nov. 11, 1950, and *Grampus* station 10352, lat. 40°00′N., long. 69°24′W., July 24, 1916, as related to standard Slope Water and Coastal Water curves.

However, in the eastern sector of the coastal region, whenever a smooth T–S curve has been observed it has conformed very closely to the standard curve. If water of these standard characteristics is formed by the mixture of Slope (S) Water and Labrador (L) Water, the ratios of constituents involved are given in Table V where the same graphical method of analysis has been

TABLE V. The constitution of Coastal Water from Slope Water and Labrador Water.

Initial σ_t	$R = L/S$	$P_L(\%)$
26.8	2.0	67
26.9	1.7	63
27.0	1.4	59
27.1	1.1	53
27.2	0.94	48
27.3	0.76	43
27.4	0.64	39
27.5	0.62	38

employed. The lighter waters show a higher content of Labrador than of Slope Water while this condition is reversed in the deeper, heavier waters. The proportion of Labrador Water involved varies from 67% to 38%. This variation is understandable when it is realized that the mixing area is much more accessible to Labrador Water from the upper 100 m. than to deeper waters. The shallower waters may flow over the Grand Banks while the deeper waters must come around the Tail of the Banks. The σ_t value for waters at about 100 m. in Labrador Water is approximately 27.2.

(F) CONSTITUENT RATIOS IN "MIXED WATER". Soule (1940b) first remarked upon the fact that the T–S relationship for waters east of the Grand Banks followed three definite co-relations, representing Labrador Water, Atlantic Current Water, and an intermediate type which he called Mixed Water. He remarked upon the scarcity of atypical stations with T–S curves oscillating between water types. The region of Mixed Water was found to be as much as 80 miles wide. An analysis of the ratios of constituents in this Mixed Water has been carried out in a manner similar to that described above. The assumption made was that Mixed Water is formed from Slope Water (similar in T–S characteristics to Atlantic Current Water as observed by Soule) and Labrador Water. The results of this analysis are given in Table VI. Again one is struck by the constancy of

TABLE VI. The constitution of Mixed Water from Slope Water to Labrador Water.

Initial σ_t	$R = L/S$	$P_L(\%)$
27.0	1.9	65
27.1	1.8	64
27.2	1.7	63
27.3	1.6	62
27.4	1.6	61
27.5	1.4	59
27.6	1.1	52

the ratios of Labrador to Slope Water involved. The proportion of Labrador Water varies only from 65% to 52%.

(G) IMPLICATIONS OF CONSTANT MIXING RATIOS. There is nothing remarkable in the concept that Slope Water is formed from the mixture of Atlantic and Coastal Waters, that Coastal Water is formed from the mixture of Labrador and Slope Waters, or that Soule's Mixed Water is formed from the mixture of Labrador and Slope (Atlantic Current) Waters. The remarkable thing is the constancy of the T–S relationship within each of the derived water masses. It appears as though there were a preferred end point in the lateral mixing of each pair of water masses.

If, as above, one postulates a system of straight-line mixing of waters from the same σ_t surfaces, one is struck by the constancy throughout the vertical column of the proportions in which the parent waters are mixed to produce "Slope" and "Mixed" Waters. Herein, perhaps, lies the explanation of the characteristic T–S curves. It seems possible that the parent waters are fed into the mixing systems as complete columns and that the proportions are strictly regulated by the dynamics of the system. This hypothesis is strengthened by the fact that the variation from constant proportions observed in the case of the production of Coastal Water from Labrador and Slope Waters is just what would be expected considering the relative accessibility of the mixing area to the parent water masses from different depths.

It is of interest to note that the type of mixing postulated as taking place between Central Atlantic and Labrador or Coastal Water gives rise to mixing

lines which come close to paralleling parts of the Central Atlantic curve (see Fig. 5). This gives rise to a Slope Water curve which, though it represents water which is only about 80% Central Atlantic water, resembles very closely the Central Atlantic curve. Reference to Fig. 4 will show that waters of any density involved in the mixing come from a much greater depth in the Central Atlantic than in the Coastal Water. However, water of the required density is found at lesser depths on the shoreward side of the Gulf Stream, consistent with the slope of the σ_t surfaces across the stream. Due to the relationship between the Central Atlantic T–S curve and the mixing lines, Slope Water will most closely resemble Atlantic Water from an even greater depth than that associated with the parent Atlantic Waters. An effect which might be incorrectly attributed to upwelling is thus produced by mixing.

The relationship between the five water masses discussed (Fig. 4) in so far as their formation is concerned is illustrated in block diagram form in Fig. 7.

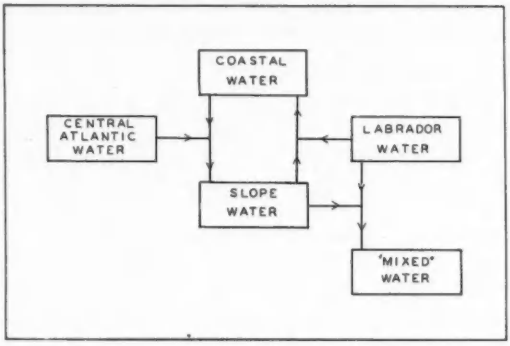

FIG. 7. Block diagram showing relationship between water masses north of the Gulf Stream.

II. CURRENTS IN THE SLOPE WATER

WATER MOVEMENT ON THE SCOTIAN SHELF

The discharge of land drainage into the Coastal Waters maintains a surface layer of low salinity with density inferior to that of surface layers offshore. The hydrostatic forces tend to drive this surface layer offshore, and this, coupled with the Coriolis acceleration, results in a southwesterly flow of Coastal Waters over the Scotian Shelf.

In studying the origin of the cold "intermediate" layer of the Scotian Shelf, Hachey (1938) has stressed the observed transport towards the southwest as opposed to winter chilling *in situ*. Such a southwest movement is also consistent with current patterns found by Sandstrom (1919).

Dawson (1913) has estimated that the Gaspé Current, flowing close against the southern shore of the St. Lawrence estuary, carries a volume of water equal to 95 times the volume of the St. Lawrence River outflow and that the same

volume probably rounds Cape Breton in what he has called the Cape Breton Current. If this is so, the average transport would be approximately 1×10^6 m.^{3}/sec., or sufficient to flood the whole of the Scotian Shelf as far west as the Gulf of Maine to a depth of 150 m. in some 250 days. MacGregor (1956) found outward flow from Cabot Strait as great as 2.22×10^6 m.^{3}/sec., with seasonal averages varying from 0.57×10^6 (spring) to 1.46×10^6 (summer).

The existence of a generally southwesterly flow in the Coastal Waters would appear to be well established.

The Slope Water, then, lies between the Coastal Waters with their southwesterly drift and the Gulf Stream, moving swiftly towards the northeast, and is formed by a mixing of waters from these two sources. It is of interest to investigate the systematic movements which may characterize the Slope Water.

If the wake stream theory, as propounded by Rossby (1936) and which successfully explains many features of the Gulf Stream system, is to be applied, it follows that "the compensating movements set up in the surroundings of a wake stream must appear as a counter current on the left side".

CURRENT OBSERVATIONS IN THE SLOPE WATER

Sandstrom (1919), from observations made in the summer of 1915, computed currents normal to hydrographic sections running outward from the Nova Scotia coast. His section XIII (Fig. 8) ran from station 37 near the coast to station 44 well into the Slope Water. A band of water centred some 20 to 40 miles

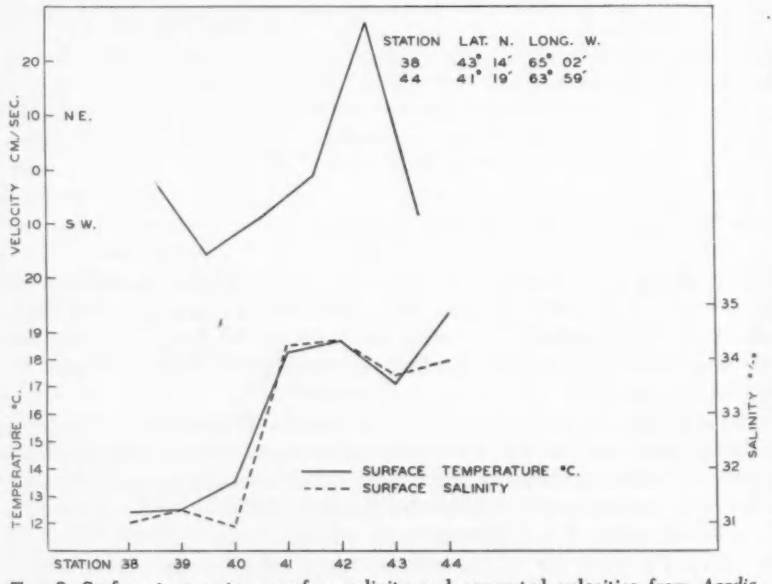

FIG. 8. Surface temperature, surface salinity and computed velocities from *Acadia* stations 38 to 44, July 21 and 22, 1915.

outside of the Slope Water boundary displayed velocities of over half a knot in a northeasterly direction while waters on either side moved towards the southwest. These velocities from Sandstrom's dynamic calculations are shown in Fig. 8, together with observed surface temperature and salinity. It may be seen that the Slope Water boundary fell between stations 40 and 41, while the high northeasterly velocity appeared between stations 42 and 43.

Fuglister (1951) has interpreted temperature observations at 200 m. to show the existence of multiple currents in the Gulf Stream system, inferring one or more currents in the Slope Water paralleling the main stream. His temperature charts also show evidence of a counter current close to the northern edge of the Gulf Stream. He has examined the dynamic topography from all available sections of deep hydrographic stations and found that most show strong easterly currents off the Continental Shelf and a counter current between these currents and the Gulf Stream.

In the results of each of the Slope Water surveys previously mentioned, well-defined bands were observed near the Slope Water boundary with velocities directed parallel to the Gulf Stream and in magnitude greater than 1 knot. These can be seen in Fig. 9 and 10 where observed velocities are plotted together with the minimum temperature above 100 m. On such a plot the Slope Water regime is bounded by the 10° and the 18° C. isotherms. In June 1952 (Fig. 10), there was also a suggestion of easterly current just inshore from the northern edge of the Gulf Stream at lat. 40°20′N., long. 52°20′W. This survey also showed a clockwise rotating eddy of Gulf Stream water within the Slope Water. Counter currents between the Gulf Stream and the Slope Water Current have not, however, been consistently observed. Other velocities in the Slope Water appear to be either offshore or onshore movements which are probably associated with wave-like movements in the Gulf Stream.

THE "ATLANTIC CURRENT" SOUTH OF THE GRAND BANKS

If, then, an easterly flowing current is a regular feature of the Slope Water, what of its observation in sections run south from the Grand Banks by the International Ice Patrol? Regularly between March and July of each year, ships of the United States Coast Guard occupy sections in the Grand Banks area in carrying out the work of the International Ice Patrol. Sections are run from the Grand Banks, across branches of the Labrador Current, and usually extend into the warmer easterly and northeasterly flowing waters of the "Atlantic Current". In particular, section *W* (Smith, Soule and Mosby, 1937), which runs south from the Tail of the Banks along the 50°W. meridian, should intercept the Slope Water if such water extends that far east, and should detect any steady currents in this region.

An examination has been made of the sections occupied by the Ice Patrol during the season of 1938 (Soule, 1940a). In the survey of April 27 to May 7, one section ran south at long. 50°W. to about lat. 41°N. The two most southerly stations 2630 and 2631, separated by a distance of 30 nautical miles, showed a computed current between stations of approximately 1.2 knots towards the east.

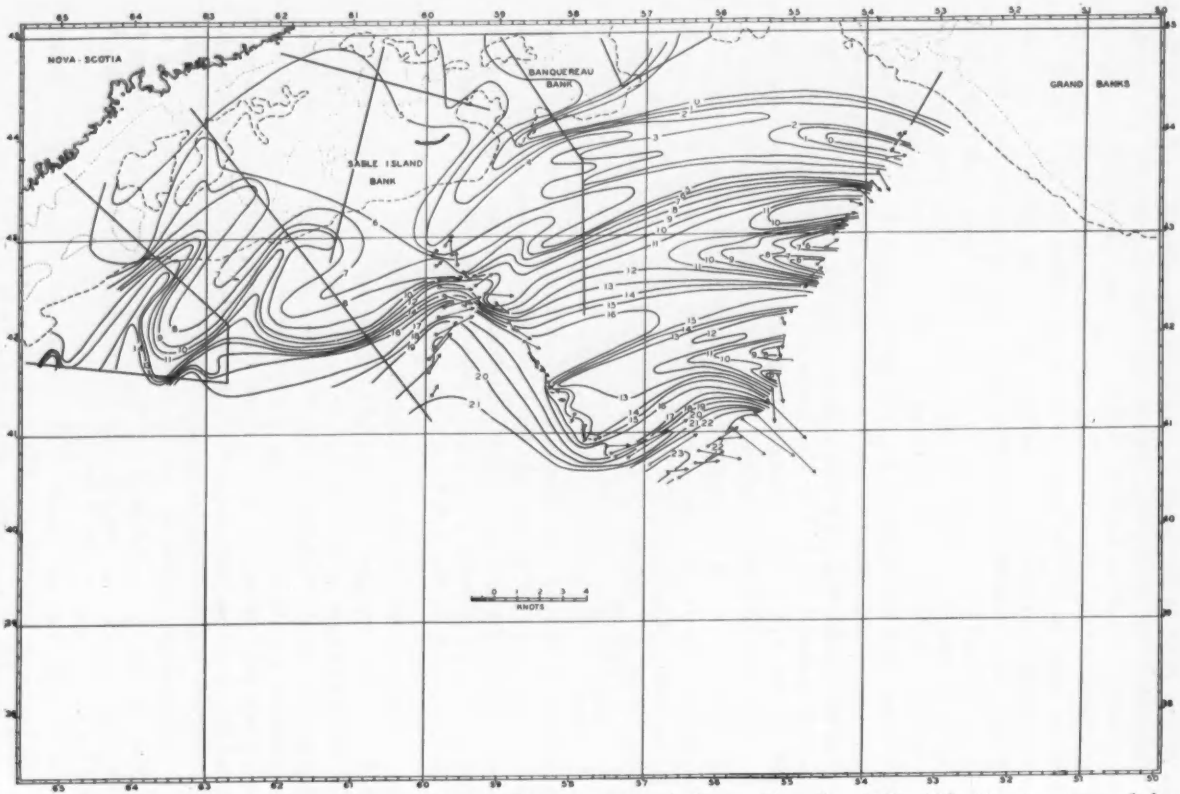

FIG. 9. Horizontal plan of minimum temperature above 100 m. as observed during November 1951. Velocities as measured by G.E.K. shown by arrows.

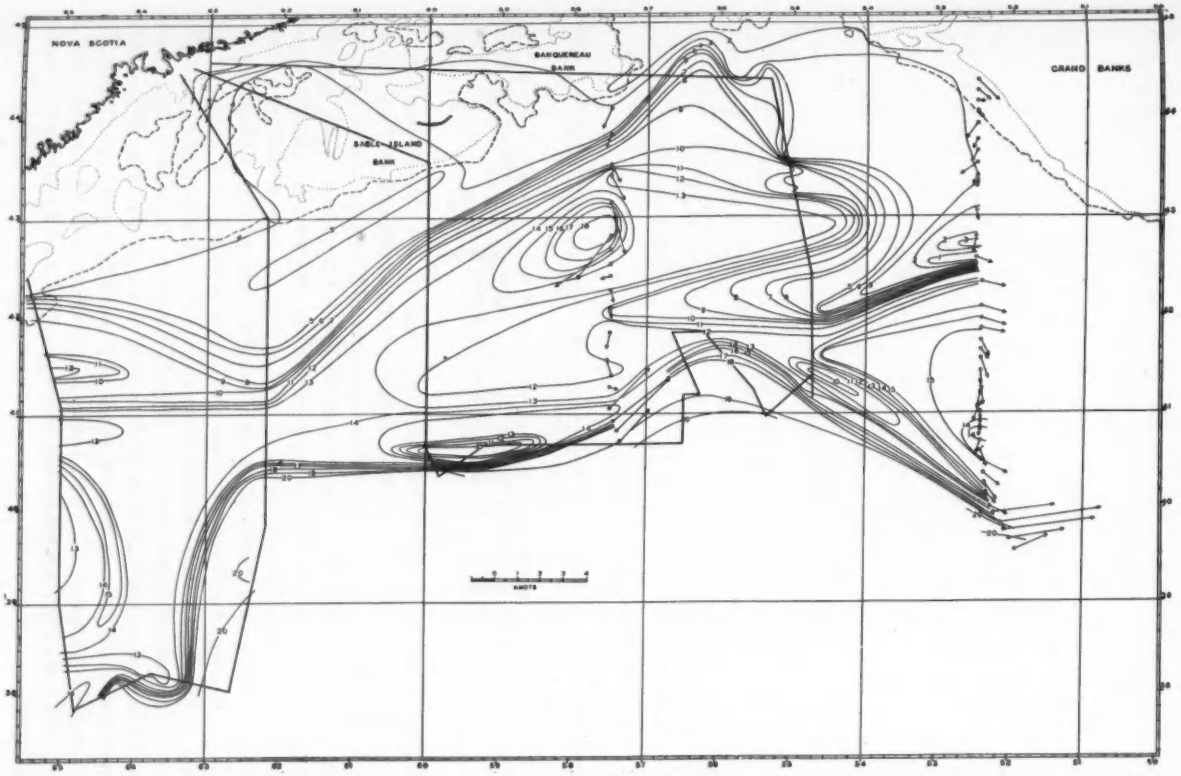

FIG. 10. Horizontal plan of minimum temperature above 100 m. as observed during June 1952. Velocities as measured by G.E.K. are shown by arrows.

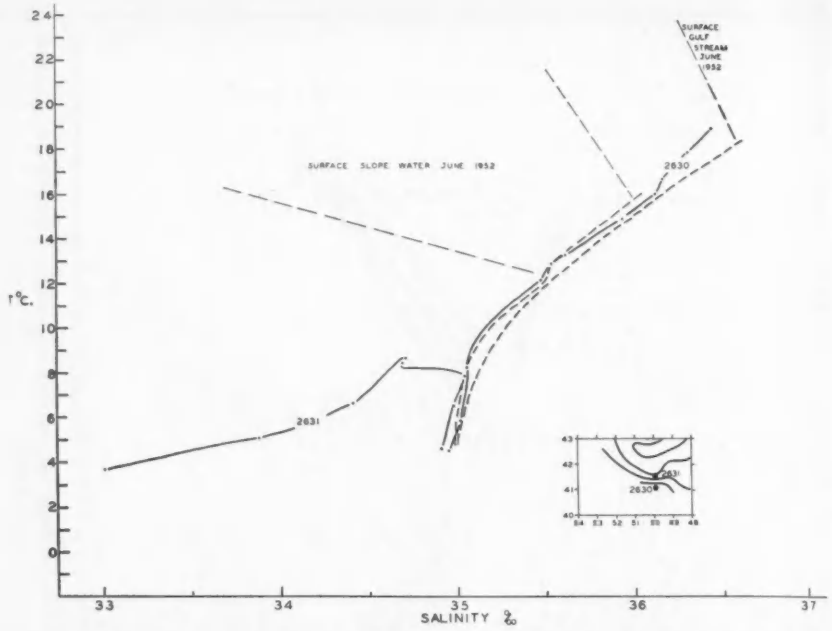

FIG. 11. T–S relations for International Ice Patrol stations 2630 at lat. 41°03′N., long. 49°57′W., May 5, 1938, and 2631 at lat. 41°33′N., long. 49°56′W., May 5, 1938. Central Atlantic and Slope Water curves are shown in dashed lines.

Temperature–salinity relationships for these stations are depicted in Fig. 11 along with the typical Slope Water and Central Atlantic curves (dashed lines) as shown in Fig. 4. The upper 100 m. at station 2630 were more saline than surface layer Slope Waters off the Scotian Shelf but below that depth the correspondence to the Slope Water curve was very close. Station 2631 showed definite Coastal or Labrador relationships. Thus an eastward current associated with the Slope Water boundary is indicated, and this current was probably of greater velocity than computed from such widely spaced stations.

In Fig. 12 are shown the T–S relationships for three stations from the survey of May 24 to June 6, 1938: stations 2717, 2718 and 2719. Station 2717 shows definite Gulf Stream characteristics as does 2718 in the upper 50 m. Below 50 m. however, station 2718 shows definite characteristics of Slope Water. Station 2719 lay in Coastal or Labrador Waters. Computed currents were 1.7 knots between stations 2717 and 2718, and 1.6 knots between 2718 and 2719, both velocities directed eastward. It may be that two separate streams were involved here or that there was a flow of Slope Water immediately inshore from the main Gulf Stream and parallel to it, the two appearing as a single wide current.

Figure 13 shows T–S relationships for three stations from the survey of

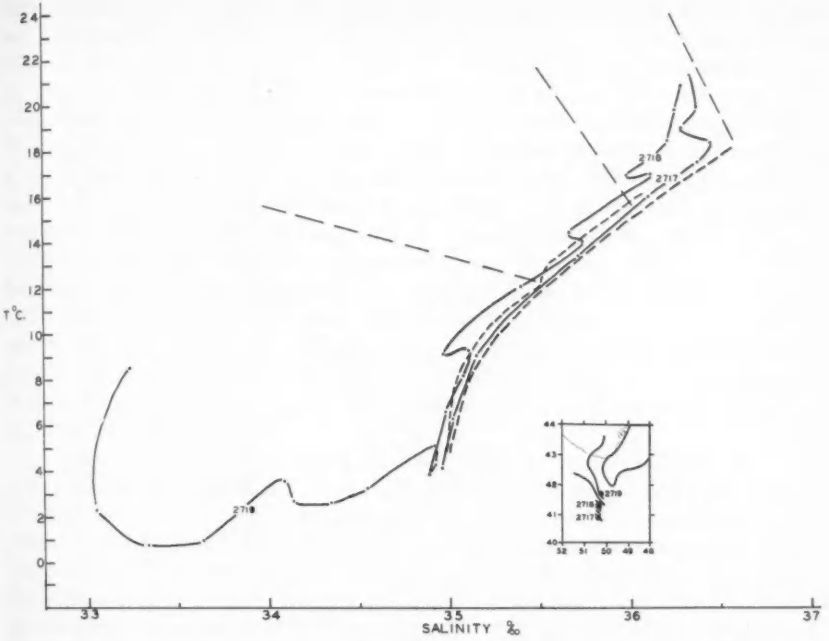

FIG. 12. T–S relations for International Ice Patrol stations 2717 at lat. 40°54′N., long. 50°23′W., June 3, 1938; 2718 at lat. 41°19′N., long. 50°20′W., June 4, 1938, and 2719 at lat. 41°41′N., long. 50°13′W., June 4, 1938. Central Atlantic and Slope Water curves are shown in dashed lines.

June 21 to July 3, 1938. Stations 2739 and 2740 lay in a band which showed southeastward velocities, the computed eastward component between them being 0.3 knot, while station 2744 was further east in a region of low northward velocities. All three stations showed T–S relations in the upper layers which closely resembled those found in the Slope Water off the Scotian Shelf in June 1952. This correspondence held to a depth of 300 m. at 2739, and 400 m. at 2740, below which waters tended towards coastal characteristics. At 300 and 400 m., the water at station 2744 showed definite Central Atlantic characteristics.

It is of interest to note the computed transport of the Labrador Current through section W at the times of these surveys. In millions of cubic metres per second, it was: April 27–May 7 survey, 5.78; May 24–June 6 survey, 2.76; June 21–July 3 survey, 5.07 (Soule, 1940a). It seems very likely that these fluctuations are associated with the passage of waves in the Gulf Stream.

At the time of each of these three surveys, there was an eastward flow, past the Tail of the Grand Banks, of waters having characteristics similar to Slope Water off the Scotian Shelf. This leads one to believe that the "Atlantic Current", as regularly observed near the southern limit of the area surveyed by

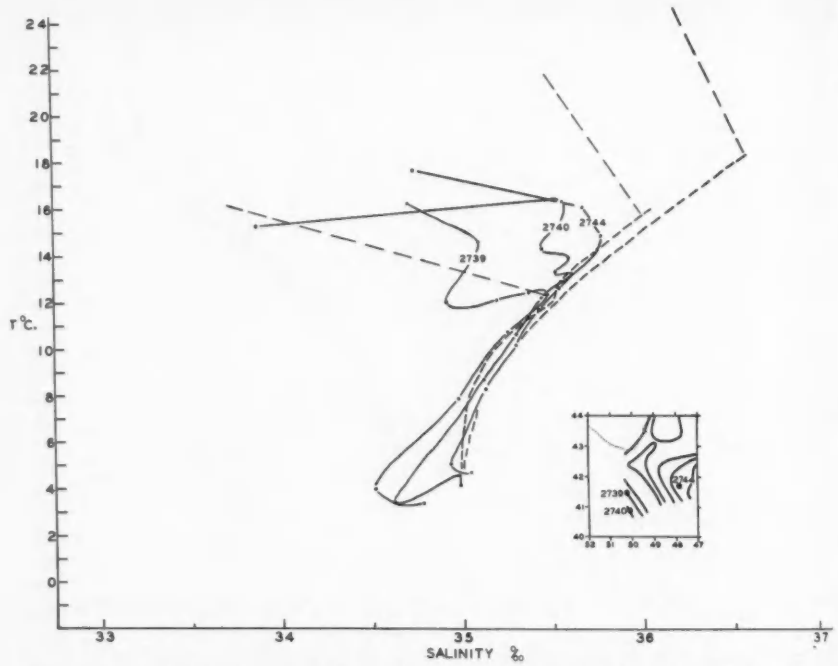

FIG. 13. T–S relations for International Ice Patrol Stations 2739 at lat. 41°28′N., long. 50°14′W., June 22, 1938; 2740 at lat. 40°53′N., long. 50°08′W., June 22, 1938, and 2744 at lat. 41°44′N., long. 47°51′W., June 24, 1938. Central Atlantic and Slope Water curves are shown in dashed lines.

the International Ice Patrol, is a flow of Slope Water rather than the continuation of the Gulf Stream, and that the Gulf Stream proper flows past the Grand Banks somewhat farther south. Such a view is supported by the observations from the Slope Water surveys as can be seen particularly well in Fig. 10 where two distinct eastward currents are shown, one associated with the Slope Water boundary and the other with the Gulf Stream edge as defined by a temperature-depth relationship as well as by T–S characteristics.

THE SUPPLY OF SLOPE WATER

The existence of an eastward flow of Slope Water would seem, then, to be fairly well established. If it is assumed that mass is conserved in the area west of the Grand Banks and north of the Gulf Stream, it is possible to make an estimate of the transport required in the Slope Water Current.

It has already been mentioned that the outflow from Cabot Strait probably carries close to 10^6 m.^{3}/sec. Only a small portion of this represents contribution from the river system, and it is probable that there is a compensating inflow on the Newfoundland side of Cabot Strait so that the net contribution to the area

under consideration will be the aggregate of drainage into the Gulf plus the net inflow through the Strait of Belle Isle. Around the Tail of the Grand Banks flows a branch of the Labrador Current which regularly contributes water to the area. In fourteen surveys between March 16 and July 15 during the years 1934 to 1938, the average flow of the Labrador Current through section W was 3.3×10^6 m.^{3}/sec. (Soule, 1940a). Another branch of the Labrador Current flows in the gully between the Grand Banks and the Newfoundland coast. This branch stream carried 0.8×10^6 m.^{3}/sec. at the time of the 1928 survey (Smith, Soule and Mosby, 1937, p. 88). It rounds Cape Race and gives rise to the generally southwest currents observed along the south coast of Newfoundland (Gulf of St. Lawrence Pilot 1946). Thus we have a supply of Coastal and Labrador Waters to the area which amounts to over 5×10^6 m.^{3}/sec., to which must be added the land drainage from Cape Breton to Cape Hatteras. Except for some portion of the Labrador Current which may re-curve south of the Grand Banks, this supply must consistently be used up in the production of Slope Waters.

From the Gulf Stream, waters are contributed to the Slope Water in various ways. Eddies of Gulf Stream water are from time to time thrown off into the Slope Water. An example of a large eddy was observed in June 1952 (Fig. 10). While such remarkable features are probably produced quite frequently, smaller eddies must be extremely common especially in the shear zone next to the Gulf Stream. The discharge of eddies as part of an exchange equilibrium between a strong current and waters to its left is a consequence of the wake stream theory as expounded by Rossby (1936), although in his paper (p. 37) it has been indicated that between Chesapeake Bay and Nova Scotia there is a net ejection of water from the Gulf Stream.

The addition of waters from these sources is partially balanced by the loss of Slope Water in cold eddies which pass southward through the Gulf Stream. An example of such an eddy was observed in detail during operation Cabot (Fuglister and Worthington, 1951). It does not seem likely that cold eddies could remove more than a small portion of the waters added to the Slope Water; and as the Slope Water regime extends southwest only as far as Cape Hatteras and is not growing indefinitely, conservation of mass requires that an eastward flowing current be a regular feature of the Slope Water.

If it is assumed that all the Labrador Water which enters the area west of the Grand Banks becomes mixed to form Slope Water and eventually escapes from the area as Slope Water, an estimate of the order of magnitude of the Slope Water Current may be formed. Taking the value 3.3×10^6 m.^{3}/sec. for the flow of the Labrador Water round the Tail of the Banks and 0.8×10^6 m.^{3}/sec. for the inshore branch around Cape Race, we have a total of some 4×10^6 m.^{3}/sec. Now the composition of Slope Water, if assumed to be formed from Atlantic and Labrador Waters, was shown to be roughly 80% Atlantic and 20% Labrador. Thus, under the above assumptions, 20×10^6 m.^{3}/sec. of Slope Water must be formed and, since the Slope Water regime is not expanding, must regularly escape as a current south of the Grand Banks. This estimate may be

somewhat high since some of the Labrador Water which rounds the Grand Banks may re-curve and escape the area without mixing. Also the inshore flow around Cape Race, being confined to the upper 200 m., may be accounted for in the lower percentage of Atlantic Water in the upper layers. However, some reliance may be placed upon the order of magnitude and an estimate of from 10×10^6 to 20×10^6 m.^{3}/sec. is probably realistic. Table VII summarizes the probable inflow to and outflow from the Slope Water area.

TABLE VII. The supply of water to the Slope Water area (in 10^6m.^{3}/sec.).

Labrador Current	
(a) Around the Tail of the Banks (varies greatly, but on the average)	+3.3
(b) Inshore branch (one estimate only)	+0.8
Cape Breton Current	+1.0
Inflow to Gulf of St. Lawrence (probably nearly balances Cape Breton Current)	−1.0
Gulf Stream eddies (based on percentage composition of Slope Water)	+16.4
Cold eddies passing south through the Gulf Stream (no estimate, but probably small)	?
TOTAL	+20.5
Slope Water current (required to balance)	−20.5

ENERGY SOURCES FOR SLOPE WATER CURRENT

Most if not all of the energy involved in the eastward flow of Slope Water must come from the Gulf Stream. The simplest mechanism is, of course, a simple frictional drag where momentum is transferred across the northern edge of the Gulf Stream with the result that the Slope Water tends to be carried along with it. The generally accepted theory for the way this transfer takes place in turbulent friction pictures the migration of eddies across the shear zone carrying with them the momentum characteristic of their source. Eddies are visualized in a whole spectrum of sizes and it is questionable if a clear distinction should be made between the eddies which give rise to turbulent friction and large eddies such as that observed in June 1952 (Fig. 10). These large eddies, besides their rotation, must bring to the Slope Water a large contribution of momentum in an easterly direction.

SUMMARY

In the Slope Water investigations a large oceanic area which was hitherto little known has been subjected to fairly detailed study. Irregularity and change typify the area where stirring and mixing take place on a gigantic scale.

The most striking feature of the area is the sharp Slope Water boundary which is subject to large-scale variations in position. Any systematic variation which may take place in this feature is yet to be observed.

A definite T–S correlation has been established for the Slope Water off the Scotian Shelf and it seems likely that this water differs significantly from Slope

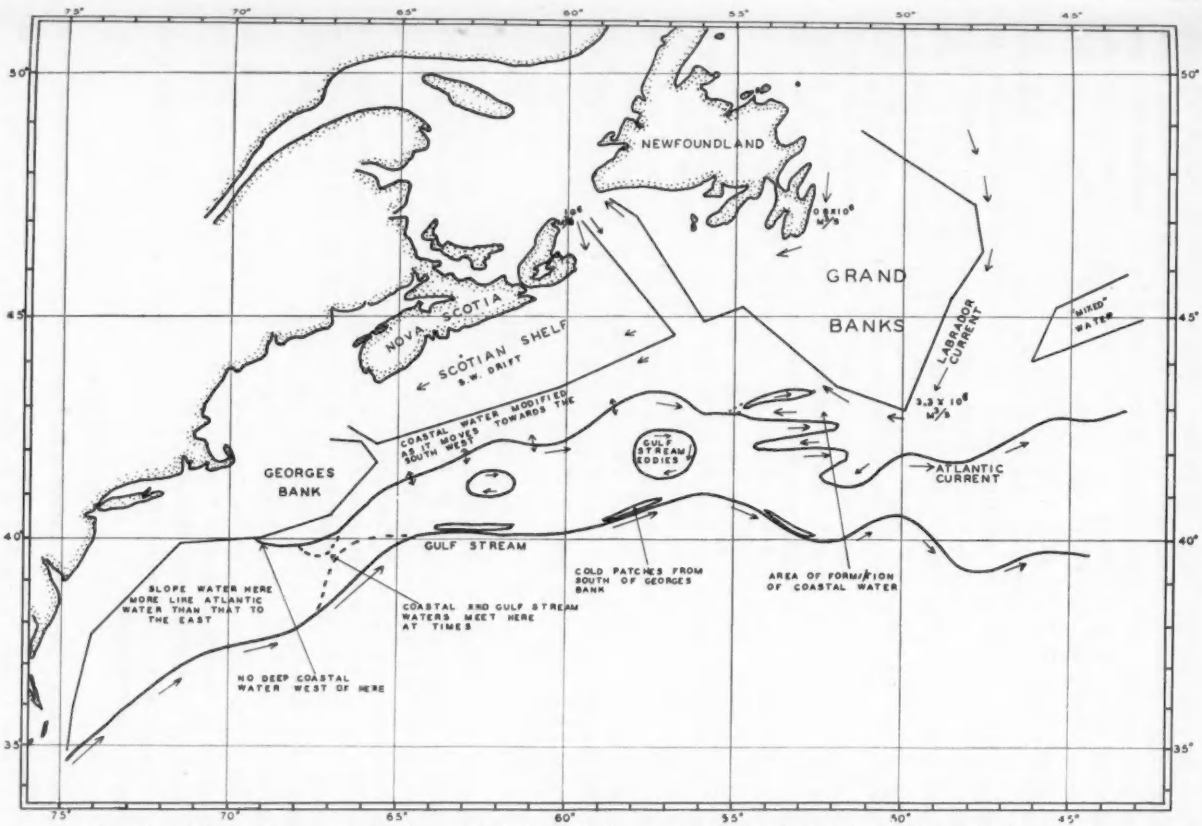
NEWFOUNDLAND
GRAND BANKS
NOVA SCOTIA
SCOTIAN SHELF
S.W. DRIFT
LABRADOR CURRENT
"MIXED" WATER
COASTAL WATER MODIFIED TOWARDS THE SOUTH WEST AS IT MOVES
GULF STREAM RODIES
GEORGES BANK
ATLANTIC CURRENT
GULF STREAM
SLOPE WATER HERE MORE LIKE ATLANTIC WATER THAN THAT TO THE EAST
COASTAL AND GULF STREAM WATERS MEET HERE AT TIMES
COLD PATCHES FROM SOUTH OF GEORGES BANK
AREA OF FORMATION OF COASTAL WATER
NO DEEP COASTAL WATER WEST OF HERE

FIG. 14. A schematic drawing showing present ideas of the nature of the Slope Water off the Scotian Shelf.

Water west of Georges Bank. When the origin of the Slope Water is sought, using realistic concepts regarding the mixing processes involved, it would appear that it is made up of Central Atlantic Water diluted by the addition of at least 20% Coastal Water—a significant amount. A similar approach to mixing ratios has shed considerable light upon the origin of Coastal Water from the mixture of Labrador and Slope Waters.

Eastward flowing currents have been regularly found in the Slope Water and, from the established T–S correlation, this current has been identified with the Atlantic Current south of the Grand Banks which has been consistently found by the International Ice Patrol. The picture of a secondary eastward current is consistent with Fuglister's multiple-current theory, but amplifies it, in that it is here shown that the secondary current carries water which is measurably unlike Gulf Stream water. The secondary current, then, is not the result of a simple bifurcation of the Gulf Stream, but a mechanism by which a mixing product formed to the left of the stream is dispersed from its region of formation. From the percentage composition of Slope Water and figures for the flow of Labrador Water into the area an estimate of the order of 10^7 m.^{3}/sec. for the transport of the Slope Water Current has been made. It does not require a great stretch of the imagination to suggest that the third current, which Fuglister (1951) infers from the temperature distribution, carries the "Mixed Water" (found east of the Grand Banks by Soule) eastward away from its area of formation.

Figure 14 summarizes schematically the picture of the Slope Water which has been built up on the basis of these and other investigations.

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